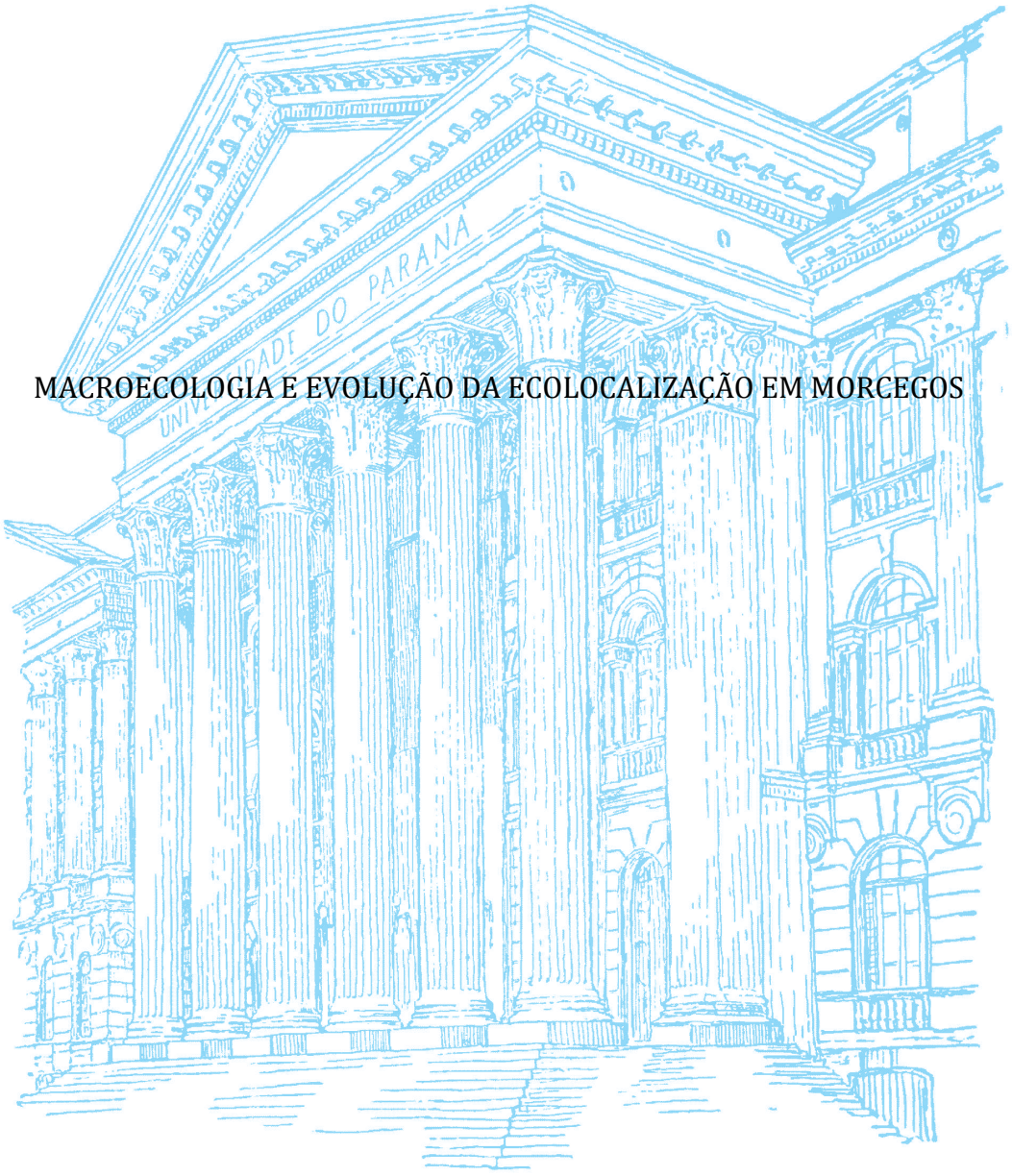
UNIVERSIDADE FEDERAL DO PARANÁ
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO

DIEGO ROBERTO BILSKI



MACROECOLOGIA E EVOLUÇÃO DA ECOLOCALIZAÇÃO EM MORCEGOS

CURITIBA
2015

UNIVERSIDADE FEDERAL DO PARANÁ
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO

DIEGO ROBERTO BILSKI

MACROECOLOGIA E EVOLUÇÃO DA ECOLOCALIZAÇÃO EM MORCEGOS

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutor em Ecologia.

Orientador: Prof. Dr. Marcio Roberto Pie
Co-orientador: Dr. M. Brock Fenton

CURITIBA
2015

Ministério da Educação
UNIVERSIDADE FEDERAL DO PARANÁ
Setor de Ciências Biológicas
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO

Ata da defesa de Tese do aluno Diego Roberto Bilski

Aos dezenove dias do mês de março de dois mil e quinze, foi realizada no Setor de Ciências Biológicas da Universidade Federal do Paraná, a defesa da tese do doutorando Diego Roberto Bilski intitulada: "MACROECOLOGIA E EVOLUÇÃO DA ECOLOCALIZAÇÃO EM MORCEGOS". A abertura teve início às 14h30 min pelo Dr. Marcio Pie, orientador e presidente da banca. O senhor Presidente apresentou ao público presente os membros da banca examinadora e em seguida passou a palavra ao aluno, para que fizesse uma apresentação sucinta de sua tese. Após a explanação oral, o aluno passou a ser arguido pelos membros da banca: Dr. Enrico Bernard, Dr. Crisóforo Fabrício Villalobos Camacho, Dr. Maurício O. Moura e Dr. Fernando de Camargo Passos. Finda a defesa da tese, o senhor presidente da banca examinadora, fez uma rápida apreciação das conclusões mais importantes dos debates realizados e comunicou que a banca iria proceder ao ato de atribuição do resultado final, reunindo-se em sessão secreta. Os trabalhos foram interrompidos por cinco minutos. Após este intervalo, foram proclamados os resultados atribuídos pela banca examinadora, que decidiu pela "..APROVACAO.....***da tese"***, tendo o candidato cumprido o artigo sessenta e cinco da Resolução 65/09 – CEPE, e o mesmo fez juz ao grau de Doutor em Ecologia e Conservação, área de concentração em Ecologia e Conservação. Como não havia nada mais a ser tratado, o Dr. Marcio Pie, presidente da banca examinadora, após informar que o candidato tem, a partir desta data, sessenta dias para a entrega da versão definitiva de sua tese, deu por encerrada a sessão. Eu, Isabela Galarda Varassin, Coordenadora do Programa de Pós-Graduação em Ecologia e Conservação, lavrei a presente ata, a qual assino juntamente com os membros examinadores. x.x.x.x.x.x.x.x.x.x.x.x.x.x.x..x.x.x.x.x.x.x.x.x.x.x.x.x.x.

Ministério da Educação
UNIVERSIDADE FEDERAL DO PARANÁ
Setor de Ciências Biológicas
PROGRAMA DE PÓS-GRADUAÇÃO EM
ECOLOGIA E CONSERVAÇÃO

PARECER

Os abaixo-assinados, membros da banca examinadora da defesa da tese, a que se submeteu **Diego Roberto Bilski** para fins de adquirir o título de Doutor em Ecologia e Conservação, são de parecer favorável à **APROVAÇÃO** do trabalho de conclusão do candidato.

Secretaria do Programa de Pós-Graduação em Ecologia e Conservação.

Curitiba, 19 de março de 2015.

BANCA EXAMINADORA:

Prof. Dr. Marcio Pie
Orientador e Presidente

Prof. Dr. Enrico Bernard
Membro

Dr. Crisóforo Fabrício Villalobos Camacho
Membro

Prof. Dr. Maurício O. Moura
Membro

Prof. Dr. Fernando de Camargo Passos
Membro

Visto:_____
Profª. Dra. Isabela Galarda Varassin
Coordenadora do PPG-ECO

Pós-Graduação em Ecologia e Conservação
Setor de Ciências Biológicas
UFPR
Universidade Federal do Paraná

Centro Politécnico – Caixa Postal 19031 – CEP: 81531-990, Curitiba/PR
Telefones: (41) 3361-1595 – Fax (41) 3266-2042 – ecologia@ufpr.
http://www.prppg.ufpr.br:8080/ecologia/

Agradecimentos

À toda minha família, por aturar meu mau humor nos últimos anos.
Ao meu orientador, por aturar minha esquisitice, longos períodos de silêncio e por me permitir trabalhar em casa.
Ao meu co-orientador, Brock Fenton, pelas discussões sobre morcegos, pós-graduação e ciência.
Também aos outros envolvidos no meu trabalho durante o período sanduíche, especialmente o Dr. Burton Lim, o colega Hao Li e a senhora responsável pela biblioteca, da qual não me recordo o nome. E também à doida que me hospedou durante esse período, Stoyanka Gerenska.
Aos amigos e colegas de laboratório, pós-graduação e vida acadêmica, especialmente à Viviane Deslandes, Gabriela Decker, Patrícia Ströher, Itiberê Bernardi, João Miranda, Andreas Meyer, Fernando Passos e Maurício Moura.
À CAPES pela concessão da bolsa e bolsa sanduíche.
Aos professores que aceitaram avaliar este manuscrito, Dr. Enrico Bernard, Dr. Fabrício Villalobos, Dr. Fernando de Camargo Passos, Dr. Maurício Osvaldo Moura e Dr^{a}. Viviane Deslandes do Nascimento.
À Carina e à PB, por me lembrarem do que é importante.

Resumo

Os morcegos constituem mais de 20% das espécies de mamíferos atualmente descritas, uma diversidade extraordinária ligada principalmente à capacidade de voo e à ecolocalização. A ecolocalização é um fenômeno presente em todas as famílias de morcegos. Das 19 famílias de morcegos atualmente reconhecidas, 18 emitem ecolocalização tonal produzida na laringe, enquanto espécies da família Pteropodidae emitem sons pulsados produzidos através de estalos da língua ou asas. Contudo, a ecolocalização em Pteropodidae é relatada para apenas algumas espécies, enquanto nas outras 18 famílias que emitem sons tonais esse sistema é ubíquo. A ecolocalização tonal é um sistema ativo relacionado principalmente com a localização espacial e navegação em ambientes escuros, mas também usada como método de detecção e classificação de itens alimentares em diversas espécies de morcegos. Diversos estudos oferecem hipóteses sobre a origem da ecolocalização, bem como hipóteses sobre a diferenciação dos chamados de ecolocalização em relação ao ambiente ocupado pelas diversas espécies de morcegos e a convergência dos tipos de chamados entre grupos filogeneticamente distantes. No entanto, pouco se sabe sobre a dinâmica de evolução da ecolocalização tonal, as influências morfológicas e ambientais sobre a diferenciação desta característica, e a ligação entre o fenômeno da ecolocalização e a excepcional riqueza de espécies de morcegos. O objetivo deste trabalho é apresentar respostas a estas questões a partir de uma perspectiva macroevolutiva e macroecológica, oferecendo uma visão geral sobre as forças intrínsecas e extrínsecas que afetam a evolução desta característica e possibilitam a diversidade de espécies e sinais de ecolocalização observados atualmente.

A questão das características morfológicas e ambientais atuantes sobre a diversidade de sinais de ecolocalização é abordada com o uso de ferramentas de biologia comparativa, determinando os sinais filogenético e espacial presentes nos diferentes parâmetros espectrais e temporais da ecolocalização e definindo a direção e magnitude das influências morfológicas e ambientais sobre cada parâmetro. O componente de história filogenética é preponderante sobre a maior parte dos parâmetros analisados, porém apenas a duração do chamado de ecolocalização apresenta um componente espacial próximo de zero. A amplitude de frequências no chamado aparece como o parâmetro com maior componente espacial, superior ao filogenético, e também apresenta a maior proporção de variação independente tanto da filogenia quanto do espaço. A frequência inicial também apresenta-se como um parâmetro relativamente mais plástico, enquanto a frequência final e a duração do chamado mostram menor variação independente e maior proporção de sinal filogenético. O pico de frequência mostra um componente filogenético intermediário entre a frequência inicial e final, e um componente independente superior ao espacial. A razão de aspecto da asa e o tamanho corporal (representado pelo tamanho de antebraço) têm as maiores influências sobre os parâmetros analisados, confirmando que animais maiores emitem chamados de frequência mais baixa e de maior duração. A temperatura também apresenta influência sobre a maioria dos parâmetros de ecolocalização, levando a frequências

mais altas e de menor duração. Os resultados confirmam algumas relações alométricas propostas em outros estudos, porém aqui controlando a autocorrelação filogenética entre as espécies, e demonstram heterogeneidade nos fatores filogenéticos e espaciais atuantes sobre o biosonar.

A relação entre os parâmetros de frequência e a duração dos chamados de ecolocalização leva à formação de algumas configurações espectro-temporais distintas, ligadas principalmente ao tipo de ambiente onde as espécies forrageiam mas também aos clados a que pertencem. Essas conformações muitas vezes são convergentes entre grupos distantes de morcegos que se utilizam de estratégias de forrageamento e/ou ocupam ambientes similares, porém não se sabe como esses casos de convergência se refletem na dinâmica de evolução das frequências de ecolocalização e sua relação alométrica com o tamanho de corpo. Avaliou-se então se essas diferentes conformações levam a diferentes taxas de evolução da frequência de máxima energia e do tamanho de antebraço, sob 18 hipóteses de cenários evolutivos que variam de uma taxa única para todos os clados até seis diferentes taxas evolutivas e convergências entre clados. A hipótese que melhor explica a variação encontrada na ecolocalização das espécies atuais de morcegos aponta quatro diferentes taxas de evolução, e apenas um caso claro de convergência nessas taxas. A grande maioria das espécies conserva a mesma taxa evolutiva encontrada no tipo de chamado apontado como ancestral aos morcegos que emitem ecolocalização tonal, enquanto alguns clados que emitem chamados de baixa amplitude de frequências apresentam taxas mais baixas ou mais elevadas em relação ao estado ancestral. O mesmo cenário explica também a variação no tamanho de antebraço, porém as taxas de diferenciação são menores do que aquelas da ecolocalização. Os resultados demonstram que apesar das convergências na relação espectro-temporal entre alguns grupos, as taxas de evolução da ecolocalização e tamanho de antebraço comumente seguem o padrão encontrado nos clados a que os grupos pertencem. A relação alométrica entre ecolocalização e tamanho corporal também se reflete nas diferenças de taxas evolutivas entre clados, porém em velocidades diferentes.

Sabe-se que a ordem Chiroptera apresenta uma forte relação entre a riqueza de espécies e a temperatura, formando um pronunciado gradiente latitudinal de riqueza ligado à conservação filogenética do nicho climático tropical. Porém os mecanismos ligando a coexistência de várias espécies em escala local com os padrões regionais de riqueza são desconhecidos. A atenuação acústica gerada pela atmosfera, uma função não linear da temperatura, umidade e frequência sonora, pode atuar como um mecanismo de facilitação da coexistência diminuindo a interferência acústica entre hetero- e coespecíficos. Essa hipótese é testada primeiramente buscando-se a melhor combinação de variáveis ambientais que explicam o gradiente de riqueza de espécies que ecolocalizam, e avaliando a capacidade desse modelo em prever a riqueza de espécies que não possuem ecolocalização tonal. Em seguida, avaliou-se o papel da atenuação sonora diretamente sobre o padrão de riqueza de espécies através de modelos generalizados aditivos. A combinação entre temperatura e umidade, variáveis responsáveis pela atenuação sonora, é a que melhor explica o gradiente de riqueza das espécies que ecolocalizam, porém este modelo prediz uma riqueza de espécies

muito maior do que a observada para as espécies que não ecolocalizam. A atenuação sonora explicitamente modelada responde por 79% da variação no gradiente de riqueza de espécies, excedendo a variação explicada simplesmente pela temperatura e umidade em separado. Esses resultados fornecem evidências de que a atenuação sonora pode ser o principal mecanismo de ligação entre os processos locais e regionais que determinam o gradiente de riqueza de espécies de morcegos que emitem ecolocalização tonal.

Abstract

Bats constitute more than 20% of the currently known mammal species, an exceptional diversity linked to powered flight and echolocation. Eighteen from the 19 bat families use tonal echolocation produced in the larynx, while species from the Pteropodidae family use tong or wing clicks in some circumstances. However, only a few species of Pteropodidae are known to produce echolocation, while tonal echolocation is ubiquitous in all species from the other 18 families. Tonal echolocation is an active system commonly used for spatial navigation in low-light conditions, but a large number of species also use it to detect and classify food items. Several studies offer hypotheses about the origin of echolocation and the differentiation between echolocation types in relation to habitat, as well as the convergence of echolocation designs among phylogenetically distant groups. However, the dynamics of the tonal echolocation evolution, the influences of morphological and environmental variables, and the mechanisms linking echolocation to the exceptional bat diversity are poorly known. This work presents answers to these questions from a macroevolutionary and macroecological perspective, offering a broad-scale assessment of the intrinsic and extrinsic forces that shape this characteristic and allow the observed diversity of species and echolocation signals.

Comparative biology tools are used to determine the morphological and environmental variables shaping the diversity of echolocation calls, establishing the phylogenetic and spatial signals in the different spectral and temporal parameters of echolocation, and analyzing the direction and magnitude of the morphological and environmental influences. The phylogenetic component is preponderant in almost all parameters analyzed, although only the call duration shows a nearly absent spatial component. Call bandwidth appears as the most spatially structured parameter, greater than the phylogenetic signal, and also has the greatest variation independent from both phylogeny and space. The initial frequency also appears as a relatively plastic characteristic, while the final frequency and call duration show the smallest independent component and a greater contribution of phylogenetic history. The peak frequency has a phylogenetic component in between that of the initial and final frequencies, and a independent component greater than the spatial one. Wing's aspect ratio and body size (represented by the forearm length) have the greatest influence over the analyzed parameters, confirming the proposition that larger species emit calls of lower frequencies and longer durations. Temperature is also influential over most of the analyzed parameters, leading to higher frequencies and lower durations in the warmest regions. The results corroborate some of the proposed allometric relationships between echolocation and body size, but here controlling for the phylogenetic autocorrelation among species, and demonstrate the heterogeneity in the phylogenetic and spatial influences over the biosonar variation.

The relationship between frequency parameters and call duration leads to some distinct spectrotemporal configurations, majorly linked to the habitat in which the species forage, but also to their phylogenetic positions. These call designs are

often convergent between distantly related groups that forage and/or occupy similar habitats, however little is known about how these cases of design convergences translate into the dynamics of evolution of echolocation frequencies and their allometric relationship with body size. This work evaluates whether these different call designs lead to different rates of frequency of maximum energy and forearm length evolution, evaluating 18 hypothetical scenarios that vary from a single rate of evolution for all bat species to a scenario of six different rates and cases of convergences between clades. The hypothesis that better explains the variation in echolocation frequencies among current bats is composed by four different rates of phenotypic differentiation and just one clear case of convergence in these rates. The vast majority of species retains the same rate of the echolocation type found to be the ancestral state of laryngeal echolocating bats, while some clades that emit narrowband calls have rates lower or higher than the ancestral background. The same scenario explains the variation in forearm length, yet with rates always lower than those found for echolocation frequency. The results show that, despite the convergences in call shape between some groups, rates of frequency and body size evolution often follow the pattern of the clades to which the groups pertain. The allometric relationship between echolocation and body size is also reflected in the rates of phenotypic differentiation, although with disparate paces.

It is known that Chiroptera shows a strong relationship between species richness and temperature, leading to a pronounced latitudinal richness gradient linked to the phylogenetic conservatism of the tropical niche. However, the mechanisms linking the coexistence of species in local scale with the regional patterns are poorly known. Atmospheric sound attenuation, a nonlinear function of temperature, humidity and sound frequency, can act as a mechanism that facilitates the coexistence through diminishing the acoustic interference between hetero- and conspecifics. This hypothesis is tested through assessing the environmental predictors that best explain the richness gradient of echolocating bats, and then evaluating the capacity of this model in predicting the richness gradient of non-echolocating species. Further, the role of atmospheric sound attenuation in shaping the echolocating species richness is directly evaluated through generalized additive models. As expected, the model composed by temperature and humidity, the variables responsible for sound attenuation, has the best fit to the richness gradient of echolocating bats, but this model greatly overpredicts the richness of non-echolocating bats. The explicitly modeled atmospheric sound attenuation accounts for 79% of the variation in the richness gradient, exceeding the variation explained by a model composed by temperature and humidity separately. These results show that sound attenuation can be the principal mechanism linking the local and regional scale processes that shape the richness gradient of laryngeal echolocating bats.

SUMÁRIO

Introdução geral

Com cerca de 1100 espécies atualmente descritas, os morcegos representam mais de 20% das espécies de mamíferos atuais (Simmons 2005a). Exceto pela ausência na Antártica, estes animais são abundantes e diversos em todos os continentes, apresentando um amplo espectro de recursos alimentares utilizados, como insetos, frutos, néctar, pequenos vertebrados, peixes e sangue (Simmons & Conway 2003). A capacidade de voo verdadeiro e a ecolocalização são tidas como as maiores responsáveis por essa grande riqueza de espécies de morcegos e pela sua capacidade em explorar diversos nichos (Jones & Teeliing 2006, Simmons 2005b).

O parco registro fossilífero de morcegos aponta para uma grande explosão adaptativa durante o Eoceno, quando teriam surgido todas as linhagens atualmente existentes (Simmons 2005b). Nessa época geológica grande parte do globo apresentava climas semelhantes ao clima tropical atual, e a distribuição dos táxons atuais de morcegos sugere a conservação deste nicho climático (Buckley *et al*. 2010). Porém essa grande radiação adaptativa em um tempo relativamente curto dificulta a proposição de filogenias baseadas exclusivamente em caracteres morfológicos (Simmons 2005b, Teeling *et al.* 2005). Com isso, as adaptações para a ecolocalização foram e continuam sendo utilizadas como caracteres determinantes para a classificação das espécies (Arita & Fenton 1997, Simmons 2005a).

Como a ecolocalização é um sistema complexo que envolve especializações nos sistemas respiratório e nervoso central, além de adaptações morfológicas nas orelhas dos morcegos (Arita & Fenton 1997, Neuweiler 2003, Vater & Kössl 2004), assumiu-se, por vários anos, que esta adaptação teria surgido uma única vez durante a evolução do grupo (Simmons 2005b). Neste cenário, um único evento seria responsável pela divisão de um grupo capaz de ecolocalizar através da laringe (Microchiroptera) e outro sem esta capacidade (Megachiroptera), composto atualmente apenas pela família Pteropodidae (Kunz & Pierson 1994; Simmons 2005b). Contudo, um gênero desta família, *Rousettus*, possui espécies capazes de

ecolocalizar através de estalos produzidos pela língua (Holland *et al.* 2004, Yovel *et al*. 2010), enquanto membros de outras subfamílias de Pteropodidae ecolocalizam através de estalos produzidos com as asas (Boonman *et al.* 2014).

No entanto, contrariando o cenário evolutivo baseado em caracteres morfológicos e de ecolocalização, abordagens baseadas em caracteres moleculares postulam a separação dos morcegos capazes de ecolocalização em duas subordens: Yangochiroptera, composta por 13 famílias, e Yinpterochiroptera, com 6 famílias (Eick *et al*. 2005; Teeling *et al.* 2005). Neste último grupo está inclusa a família Pteropodidae, antes considerada como um grupo à parte na evolução de Chiroptera (Teeling *et al.* 2000). Neste cenário mais recente, consideram-se duas possibilidades para a evolução da ecolocalização: uma origem única, com posterior perda da capacidade de ecolocalização nos Pteropodidae, e ressurgimento secundário no gênero *Rousettus* (Teeling *et al*. 2000; Simmons 2005b); ou então a existência de dois eventos de evolução da ecolocalização, uma vez no ancestral de Yangochiroptera, e outra em Yinpterochiroptera, no ancestral comum do clado que exclui os Pteropodidae (Eick *et al*. 2005). Porém este evento evolutivo ainda é motivador de diversas discussões (Jones & Holderied 2007), e a recente descoberta da ecolocalização através de estalos das asas em outras subfamílias de Pteropodidae (Boonman *et al.* 2014) deve reacender esse debate (Fenton & Ratcliffe 2014).

Essa ecolocalização em espécies de Pteropodidae, no entanto, é produzida apenas em contextos específicos como modo de localização espacial, e difere estruturalmente da ecolocalização tonal, produzida na laringe, presente nas outras 18 famílias de morcegos (Schnitzler *et al.* 2003). A ecolocalização tonal pode servir a diversos propósitos, sendo a percepção do meio físico o mais óbvio deles (Fenton 1992, Simmons & Geisler 1998), provavelmente presente em todas as espécies capazes de ecolocalizar (Jones 1999). Já a detecção e localização de presas é algo que requer maior precisão e detalhamento do que o necessário para auxiliar na movimentação e detecção de grandes obstáculos (Fenton 1992), mas acredita-se que todas as espécies utilizam a ecolocalização em algum momento da obtenção do alimento (Kunz & Pierson 1994).

Essa gama de possibilidades de uso do biosonar é refletida no amplo

espectro de frequências capazes de serem emitidas pelas espécies de morcegos, que podem estender-se de 11 kHz a mais de 200 kHz (Jones 1999). A frequência dominante (Figura 1) emitida por uma determinada espécie comumente reflete o tipo de utilização que a espécie faz do biosonar (Simmons & Conway 2003). Por exemplo, a maior parte dos morcegos insetívoros que localizam suas presas através da ecolocalização emite frequências dominantes no intervalo entre 20 kHz e 60 kHz, o intervalo de frequência ideal para localizar pequenos insetos (Jones & Holderied 2007).

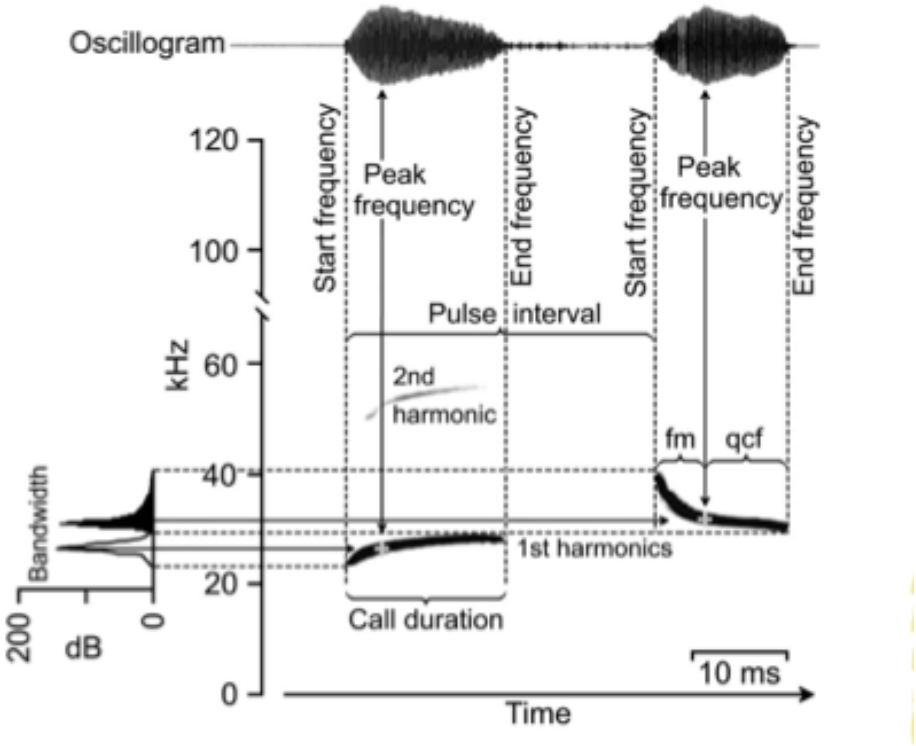


Figura 1: Parâmetros que compõem a ecolocalização, estimados a partir do espectrograma e oscilograma dos chamados em fase de busca. Extraído de Jung *et al.* 2014. Neste estudo são avaliados os parâmetros de frequência inicial, frequência final, pico de frequência, amplitude e duração.

Há diversos tipos de estratégias de ecolocalização encontrados em morcegos (Figura 2). Basicamente, estas estratégias podem ser categorizadas em três grupos, em relação à frequência e tempo de duração dos pulsos: (1) sinais de espectro amplo, que englobam uma grande quantidade de frequências e normalmente

emitidos por um curto período de tempo (<5ms); (2) sinais de espectro reduzido, que distribuem-se por uma pequena faixa de frequências e comumente são mantidos por um longo período; e (3) sinais de frequência constante, mantidos por longos períodos de tempo (±60ms) em uma única frequência, permitindo a "classificação" do eco recebido pelos morcegos (Jones 2005). Esses tipos de sinais têm relação direta com o tipo de habitat onde as espécies forrageiam e/ou se deslocam (Figura 3; Schnitzler & Kalko 2001, Schnitzler *et al.* 2003). O intervalo entre os pulsos de ecolocalização, e em alguns casos também a estrutura, diferem de acordo com fases de detecção. A fase de busca caracteriza-se por intervalos mais longos, que gradualmente diminuem quando da aproximação em relação ao alimento até a formação de fases terminais (*terminal buzzes*), próximo da captura ou coleta do alimento (Griffin *et al.* 1960).

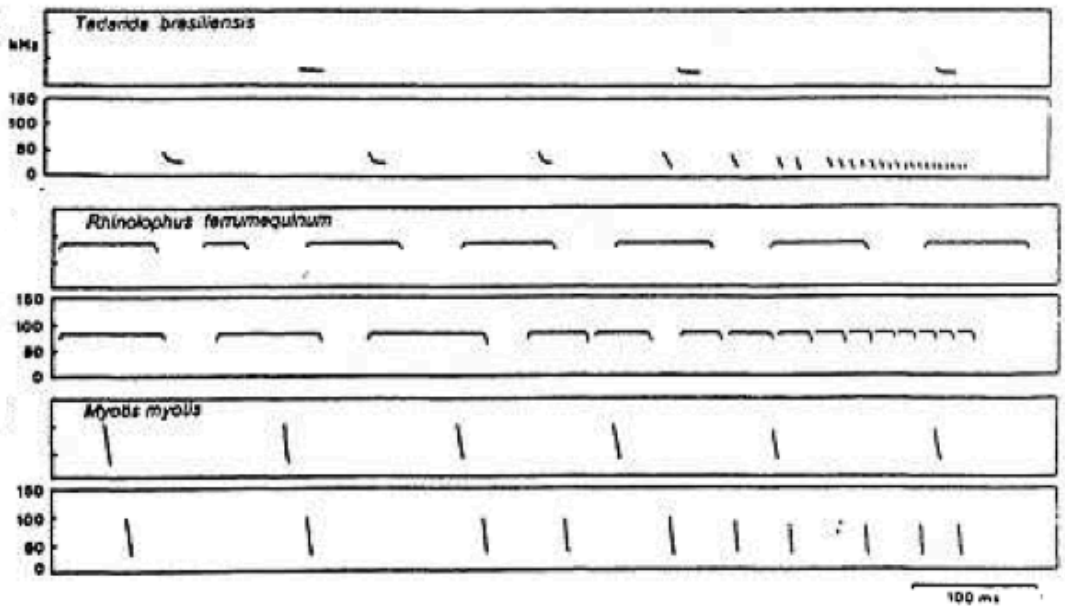


Figura 2: Padrões espectro-temporais (kHz x ms) em fase de busca (acima) e em fase terminal (abaixo) em três espécies de morcegos insetívoros. Em fase de busca, podem ser observados, respectivamente, exemplos de sinais de espectro reduzido (*Tadarida brasiliensis*), frequência constante (*Rhinolophus ferrumequinum*) e espectro amplo (*Myotis myotis*). Modificado de Schnitzler & Kalko 2001.

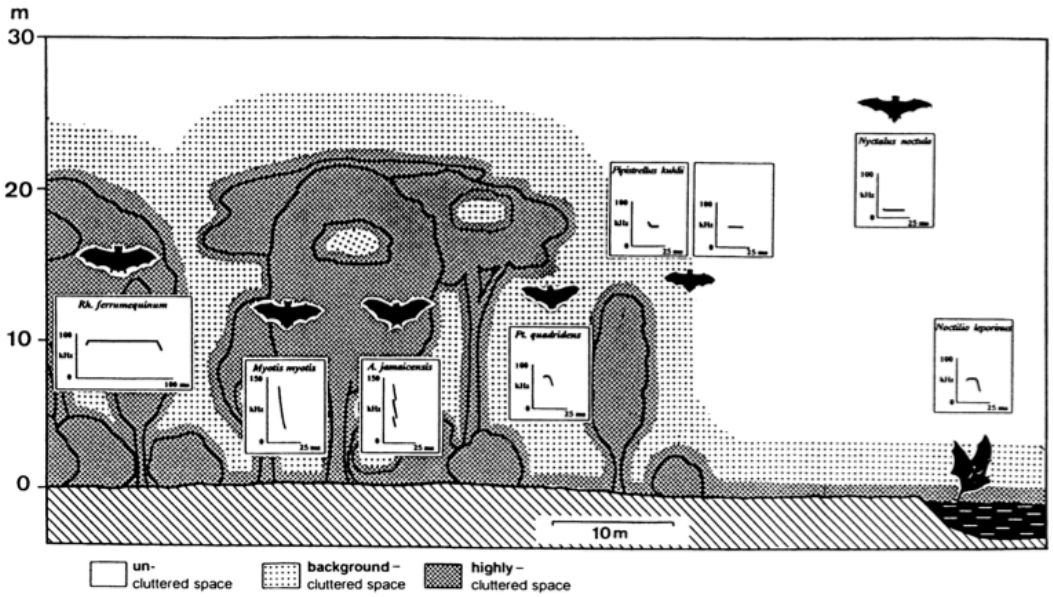


Figura 3: Esquema simplificado da relação entre os padrões espectro-temporais de ecolocalização e o tipo de habitat utilizado pelas espécies. Os habitats dividem-se de acordo com a densidade da vegetação, caracterizando ambientes totalmente abertos, onde prevalecem ecolocalizações de baixa frequência e espectro reduzido; ambientes próximos à borda da vegetação e próximos ao solo e corpos d'água, onde predominam sinais de espectro reduzido e frequências altas; e ambientes de dominados por vegetação, onde sinais de espectro amplo e frequência constante são mais comuns. Extraído de Schnitzler & Kalko 2001.

A ecolocalização é um processo energeticamente dispendioso, com o custo energético para a emissão de pulsos de ecolocalização equiparável ao custo energético do voo nestes animais (Speakman *et al*. 1989). Porém, de acordo com experimentos realizados com algumas espécies, acredita-se que a maioria dos morcegos sincroniza a emissão de pulsos com o movimento das asas, o que praticamente anula o custo energético da emissão dos pulsos, pois os mesmos grupos musculares são utilizados nos dois processos (Rayner 1991; Speakman & Racey 1991, Voigt & Lewontin 2012). Com vistas à economia de energia, portanto, a taxa ótima de emissão de pulsos seria regulada pelo tamanho dos animais, ou talvez mais especificamente pelo tamanho de suas asas (Jones 1999, Holderied & von Helversen 2003). Além disso, a frequência da ecolocalização apresenta também uma

relação negativa com o tamanho da espécie, por conta das cordas vocais mais longas em animais maiores (Jones 1999).

Além do tamanho dos animais e dos custos energéticos, fatores ambientais e as propriedades físicas do som exercem também pressão seletiva sobre a ecolocalização em morcegos (Lawrence & Simmons 1982, Snell-Rood 2012). Frequências mais baixas, apesar de menos dispendiosas energeticamente, são incapazes de prover detalhes precisos e, portanto, seriam de pouca utilidade para espécies que capturam insetos em voo (Jones 1999, Fenton *et al.* 1998). Por outro lado, frequências mais altas são atenuadas pelo ar e pela umidade mais rapidamente, o que diminui a distância de alcance da ecolocalização (Fenton 1992, Stilz & Schnitzler 2012). Com isso, morcegos enfrentam um *trade-off* entre detalhamento e alcance de seu biosonar.

Comunidades de morcegos nas regiões tropicais podem conter mais de 50 espécies (e.g. Kingston *et al*. 2000), o que leva a questões sobre os mecanismos de coexistência, pois há a necessidade individual de reconhecimento do próprio pulso de ecolocalização (Obrist 1995, Barclay 1999). Além disso, sabe-se que a ecolocalização é também utilizada na determinação de espaçamento inter-individual durante o forrageio (Altringham & Fenton 2003), e a partilha do nicho acústico entre as espécies é reconhecida em diversas comunidades (e.g. Heller & von Helversen 1989, Kingston *et al.* 2000, Russo *et al.* 2007). Diferenças nos padrões de ecolocalização capacitam as espécies a forragearem a diferentes distâncias da vegetação (Siemers & Shnitzler 2004, Schmieder *et al.* 2012), mas não necessariamente revelam diferenças na utilização de recursos alimentares. Ao contrário, podem estar apenas refletindo a necessidade de reconhecimento da ecolocalização por parte da espécie (Kingston *et al*. 2001). Mais que isso, esses padrões podem também apontar a existência de diferenças entre espécies morfologicamente similares (Jones & Parijs 1993; Kingston *et al.* 2001).

Apesar de ser reconhecido que a ecolocalização apresenta padrões espécie-específicos (Simmons & Conway 2003; Teeling *et al*. 2000), até o momento as perspectivas filogenéticas existentes sobre este processo são baseadas principalmente em revisões não sistematizadas, e o abordaram ou através de

padrões muito generalizados, que consideram apenas características comuns dentro das famílias de Chiroptera (e.g. Eick *et al.* 2005, Jones & Teeling 2006), ou então em estudos de comunidades pontuais (e.g. Kingston *et al*. 2000), que não refletem satisfatoriamente a filogenia dos grupos. Do mesmo modo, as relações alométricas da ecolocalização com a morfologia são descritas sem levar em conta as relações filogenéticas entre as espécies (e.g. Aldridge & Rautenbach 1987, Norberg & Rayner 1987, Jones 1999), o que compromete o poder estatístico das análises utilizadas nestes estudos (Harvey & Pagel 1991, Diniz-Filho 2000).

Caracteres fenotípicos comuns às espécie de um clado geralmente remontam a uma origem única, e as variações interespecíficas nesses caracteres muitas vezes são proporcionais ao tempo de divergência entre as linhagens (Felsenstein 1985). Dessa forma, as espécies não constituem amostras independentes para fins estatísticos, e análises que levam em conta esta autocorrelação filogenética devem ser usadas em estudos comparativos (Felsenstein 1985, Harvey & Pagel 1991). Pares de espécies filogeneticamente mais próximos, portanto, geralmente são mais similares entre si do que com espécies filogeneticamente mais distantes (Blomberg *et al.* 2003), um padrão definido como sinal filogenético (revisado em Munkemüller *et al.* 2012). As métricas mais utilizadas para quantificar o sinal filogenético avaliam o grau em que a variação interespecífica pode ser predita pelo tempo de divergência entre as linhagens (Pagel 1999, Freckleton *et al.* 2002, Blomberg *et al.* 2003, Munkemüller *et al.* 2012). Do mesmo modo, se um dado caráter evolui em resposta a variáveis ambientais, espécies que ocupam regiões geograficamente próximas podem ser mais similares entre si do que com espécies que ocupam regiões mais distantes (Lennon 2000, Freckleton & Jetz 2009), e uma medida da autocorrelação espacial deve ser levada em conta para controlar os efeitos da variação que se devem à proximidade geográfica entre as espécies (Diniz-Filho *et al.* 2007, Freckleton & Jetz 2009).

Portanto, a investigação sobre as variáveis que influenciam na evolução de um caráter, bem como dos processos evolutivos responsáveis pelas diferenças entre espécies e clados, requer a inclusão do conhecimento sobre as relações filogenéticas entre as espécies. No entanto, até o momento poucos estudos sobre a evolução de

morcegos se utilizaram da informação filogenética de forma direta (e.g. Davies *et al.* 2013, Jacobs *et al.* 2014), e estudos sobre a evolução da ecolocalização para a ordem Chiroptera como um todo ainda são inexistentes. Dessa forma, o presente estudo visa integrar a informação filogenética para quantificar os sinais filogenético e espacial nos diferentes parâmetros da ecolocalização (Figura 1), bem como avaliar as influências morfológicas e ambientais sobre a variação fenotípica nesses parâmetros; analisar a dinâmica de evolução do pico de frequência e sua relação com o tamanho de corpo; e investigar a ligação entre a ecolocalização e os padrões globais de diversidade de espécies de morcegos.

Referências bibliográficas:

Aldridge, H. & Rautenbach, I.L. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. *J. Anim. Ecol.* **56**: 763–778.

Altringham, J.D. & Fenton, M.B. 2003. Sensory ecology and communication in the Chiroptera. In: *Bat Ecology* (T. H. Kunz & M. B. Fenton, eds), pp. 90–127.

Arita, H.T. & Fenton, M.B. 1997. Flight and echlocation in the ecology and evolution of bats. *Trends Ecol. Evol.* **12**: 53–58.

Barclay, R.M.R. 1999. Bats are not birds: a cautionary note on using echolocation calls to identify bats: a comment. *J. Mammal.* 290–296.

Blomberg, S.P., Garland, T. & Ives, A.R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution.* **57**: 717–745.

Boonman, A., Bumrungsri, S. & Yovel, Y. 2014. Nonecholocating Fruit Bats Produce Biosonar Clicks with Their Wings. *Curr. Biol.* **24**: 2962–2967.

Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B., Harrison, S.P., Anacker, B.L., *et al.* 2010. Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proc. R. Soc. B Biol. Sci.* **277**: 2131–2138.

Diniz-Filho, J.A.F. 2000. *Métodos Filogenéticos Comparativos*. Holos, Ribeirão Preto.

Diniz-Filho, J.A.F., Bini, L.M., Rodriguez, M.A., Rangel, T. & Hawkins, B.A. 2007. Seeing the forest for the trees: partitioning ecological and phylogenetic components of Bergmann's rule in European Carnivora. *Ecography.* **30**: 598.

Eick, G.N., Jacobs, D.S. & Matthee, C.A. 2005. A Nuclear DNA Phylogenetic Perspective on the Evolution of Echolocation and Historical Biogeography of Extant Bats (Chiroptera). *Mol Biol Evol* **22**: 1869–1886.

Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* **125**: 1–15.

Fenton, M.B. 1992. *Bats*. Facts on File, New York.

Fenton, M.B., Portfors, C. V, Rautenbach, I.L. & Waterman, J.M. 1998. Compromises: Sound frequencies used in echolocation by aerial-feeding bats. *Can. J. Zool.* **76**: 1174–1182.

Fenton, M.B. & Ratcliffe, J.M. 2014. Sensory Biology: Echolocation from Click to Call, Mouth to Wing. *Curr. Biol.* **24**: R1160–R1162.

Freckleton, R.P., Harvey, P.H. & Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**: 712–726.

Freckleton, R.P. & Jetz, W. 2009. Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proc. R. Soc. B Biol. Sci.* **276**: 21–30.

Griffin, D.R., Webster, F.A. & Michael, C.R. 1960. The echolocation of flying insects by bats. *Anim. Behav.* **8**: 141–154.

Harvey, P.H. & Pagel, M.D. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford.

Heller, K.-G. & Helversen, O. v. 1989. Resource partitioning of sonar frequency bands in rhinolophoid bats. *Oecologia* **80**: 178–186.

Holderied, M.W. & von Helversen, O. 2003. Echolocation range and wingbeat period match in aerial-hawking bats. *Proc. R. Soc. London. Ser. B Biol. Sci.* **270**: 2293–2299.

Holland, R.A., Waters, D.A. & Rayner, J.M. V. 2004. Echolocation signal structure in the Megachiropteran bat *Rousettus aegyptiacus* Geoffroy 1810. *J. Exp. Biol.* **207**: 4361–4369.

Jacobs, D.S., Bastian, A. & Bam, L. 2014. The influence of feeding on the evolution of sensory signals: a comparative test of an evolutionary trade-off between masticatory and sensory functions of skulls in southern African Horseshoe bats (Rhinolophidae). *J. Evol. Biol.* **27**: 2829–2840.

Jones, G. 2005. Echolocation. *Curr. Biol.* **15**: R484–R488.

Jones, G. 1999. Scaling of echolocation call parameters in bats. *J Exp Biol* **202**: 3359–3367.

Jones, G. & Holderied, M.W. 2007. Bat echolocation calls: adaptation and convergent evolution. *Proc. R. Soc. B Biol. Sci.* **274**: 905–912.

Jones, G. & Parijs, S.M. Van. 1993. Bimodal Echolocation in Pipistrelle Bats: Are Cryptic Species Present? *Proc. R. Soc. London. Ser. B Biol. Sci.* **251**: 119–125.

Jones, G. & Teeling, E.C. 2006. The evolution of echolocation in bats. *Trends Ecol. Evol.* **21**: 149–156.

Jung, K., Molinari, J. & Kalko, E.K. V. 2014. Driving Factors for the Evolution of Species-Specific Echolocation Call Design in New World Free-Tailed Bats (Molossidae). *PLoS One* **9**: e85279

Kingston, T., Jones, G., Zubaid, A. & Kunz, T.H. 2000. Resource partitioning in rhinolophoid bats revisited. *Oecologia* **124**: 332–342.

Kingston, T., Lara, M.C., Jones, G., Akbar, Z., Kunz, T.H. & Schneider, C.J. 2001. Acoustic divergence in two cryptic Hipposideros species: a role for social selection? *Proc. R. Soc. London. Ser. B Biol. Sci.* **268**: 1381–1386.

Kunz, T.H. & Pierson, E.D. 1994. Bats of the world: An introduction. In: *Walker's Bats of the World* (R. M. Nowak, ed), pp. 1–46. Johns Hopkins University Press, Baltimore.

Lawrence, B.D. & Simmons, J.A. 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J. Acoust. Soc. Am.* **71**: 585–590.

Lennon, J.J. 2000. Red-shifts and red herrings in geographical ecology. *Ecography.* **23**: 101–113.

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., *et al.* 2012. How to measure and test phylogenetic signal. *Methods Ecol. Evol.* **3**: 743–756.

Neuweiler, G. 2003. Evolutionary aspects of bat echolocation. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **189**: 245–256.

Norberg, U.M. & Rayner, J.M. V. 1987. Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation. *Philos. Trans. R. Soc. London. B, Biol. Sci.* **316**: 335–427.

Obrist, M.K. 1995. Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. *Behav. Ecol. Sociobiol.* **36**: 207–219.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* **401**: 877–884.

Rayner, J. 1991. The cost of being a bat. *Nature* **350**: 383–384.

Russo, D., Mucedda, M., Bello, M., Biscardi, S., Pidinchedda, E. & Jones, G. 2007. Divergent echolocation call frequencies in insular rhinolophids (Chiroptera): a case of character displacement? *J. Biogeogr.* **34**: 2129–2138.

Schmieder, D.A., Kingston, T., Hashim, R. & Siemers, B.M. 2012. Sensory constraints on prey detection performance in an ensemble of vespertilionid understorey rain forest bats. *Funct. Ecol.* **26**: 1043–1053.

Schnitzler, H.-U., Moss, C.F. & Denzinger, A. 2003. From spatial orientation to food acquisition in echolocating bats. *Trends Ecol. Evol.* **18**: 386–394.

Schnitzler, H.U. & Kalko, E.K. V. 2001. Echolocation by insect-eating bats. *Bioscience* **51**: 557–569.

Siemers, B.M. & Schnitzler, H.-U. 2004. Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature* **429**: 657–661.

Simmons, N.B. 2005a. An Eocene Big Bang for Bats. *Science.* **307**: 527–528.

Simmons, N.B. 2005b. Order Chiroptera. In: *Mammal Species of the World: a taxonomic and geographic reference* (D. E. Wilson & D. M. Reeder, eds), pp. 312–529. Johns Hopkins University Press.

Simmons, N.B. & Conway, T.M. 2003. Evolution of ecological diversity in bats. In: *Bat Ecology* (T. H. Kunz & M. B. Fenton, eds), pp. 493–535. The University of Chicago Press, Chicago.

Simmons, N.B. & Geisler, J.H. 1998. Phylogenetic relationships of Icaronycteris, Archaeonycteris, Hassianycteris, and Palaeochiropteryx to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. Bulletin of the AMNH; no. 235. [New York]: American Museum of Natural History.

Snell-Rood, E.C. 2012. The effect of climate on acoustic signals: Does atmospheric sound absorption matter for bird song and bat echolocation? *J. Acoust. Soc. Am.* **131**: 1650–1658.

Speakman, J.R., Anderson, M.E. & Racey, P.A. 1989. The energy cost of echolocation in pipistrelle bats (Pipistrettus pipistrellus). *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **165**: 679–685.

Speakman, J.R. & Racey, P.A. 1991. No cost of echolocation for bats in flight. *Nature* **350**: 421–423.

Stilz, W.-P. & Schnitzler, H.-U. 2012. Estimation of the acoustic range of bat echolocation for extended targets. *J. Acoust. Soc. Am.* **132**: 1765–1775.

Teeling, E.C., Scally, M., Kao, D.J., Romagnoli, M.L., Springer, M.S. & Stanhope, M.J. 2000. Molecular evidence regarding the origin of echolocation and flight in bats. *Nature* **403**: 188–192.

Teeling, E.C., Springer, M.S., Madsen, O., Bates, P., O'Brien, S.J. & Murphy, W.J. 2005. A Molecular Phylogeny for Bats Illuminates Biogeography and the Fossil Record. *Science.* **307**: 580–584.

Vater, M. & Kössl, M. 2004. The ears of whales and bats. In: *Echolocation in bats and dolphins* (J. A. Thomas, C. F. Moss, & M. Vater, eds), pp. 89–99.

Voigt, C. & Lewanzik, D. 2012. "No cost of echolocation for flying bats" revisited. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **182**: 831–840.

Yovel, Y., Falk, B., Moss, C.F. & Ulanovsky, N. 2010. Optimal Localization by Pointing Off Axis. *Science.* **327**: 701–704.

CAPÍTULO 1

HISTORICAL AND SPATIAL STRUCTURES IN BAT ECHOLOCATION

1.1 Introduction

Bats constitute more than 20% of mammalian species (Simmons 2005a), an exceptional diversity assumed to be linked to the evolution of powered flight and echolocation (Simmons 2005b, Teeling *et al.* 2005, Jones & Teeling 2006). Almost 85% of all bat species emit tonal echolocation signals produced in the larynx (Schuller & Moss 2004), while some species in Pteropodidae, the one family that do not produce laryngeal echolocation, use tongue or wing clicks to navigate in darkness (Gould 1988, Yovel *et al.* 2010, Boonman *et al.* 2014). Most laryngeal echolocators use it to navigate and recognize ambient features at low or absent light (Griffin 1946, Moss & Surlykke 2010, Boonman *et al.* 2013), but many species also use echolocation to find and track prey items (Griffin *et al.* 1960, Korine & Kalko 2005). Echolocation calls often have species-specific components (O'Farrell *et al.* 1999, Russo & Jones 2002, Schnitzler *et al.* 2003), generating a diversity of echolocation signals linked to foraging habitat (Schnitzler & Kalko 2001, Schnitzler *et al.* 2003), food acquisition (Denzinger & Schnitzler 2013) and phylogenetic history (Jones & Teeling 2006). However, despite the recognition that phylogenetic relationships are responsible for part of the echolocation similarities among species (Jones & Holderied 2007, Jones & Siemers 2010), a formal quantification of the amount of phylogenetic signal (Blomberg *et al.* 2003, Münkemüller *et al.* 2012) is lacking.

Phylogenetic signal can be defined as the tendency of closely related species to resemble each other more than they resemble species drawn at random from the tree (Blomberg & Garland 2002). This phenomenon can result simply from the hierarchical structure of the tree, and do not require evolutionary processes like adaptation and natural selection (Hansen & Martins 1996, Blomberg & Garland 2002). Several metrics to quantify this phylogenetic dependency among species have been proposed (reviewed and evaluated in Nunn 2011, Münkemüller *et al.* 2012), among which two stand out by providing indices that can be directly compared among phylogenies: Pagel's λ (Pagel 1999, Freckleton *et al.* 2002) and Blomberg's K (Blomberg *et al.* 2003). Both indices are based on a Brownian motion

model of character evolution, where the variance in trait values is proportional to the time of divergence among taxa (Felsenstein 1985). Because of this phylogenetic dependency, statistical analyses of interspecific data must take into account the phylogenetic relatedness among species to circumvent the non-independence in species observations (Felsenstein 1985, Harvey & Pagel 1991, Revell 2010). Likewise, species that share a common habitat can show more similarities than a random pair of species, due to their similar environment (Lennon 2000, Diniz-Filho *et al.* 2007), and thus a quantification of both phylogenetic and spatial signals can help to understand the processes that shape phenotypic diversity through disentangling these sources of autocorrelation (Freckleton & Jetz 2009; Cooper *et al.* 2011).

To effectively probe the environment and localize food through the biosonar, bats need to integrate several sources of echoes to form a detailed image of the surroundings and the focused food item (Moss & Surlykke 2010). This is achieved through adaptations in the timing, frequency, intensity, duration, and sonar beam shape (Surlykke *et al.* 2009, Moss & Surlykke 2010, Jakobsen *et al.* 2012). The foraging habitat and functional guild are regarded to have prominent roles in determining the structural relationship between frequency and time within calls (Schnitzler & Kalko 2001, Surlykke & Kalko 2008, Denzinger & Schnitzler 2013), leading to cases of convergent call designs among distantly related groups (Jones & Teeling 2006). Despite these habitat-associated similarities, species often differ in some components in species-specific manners (Fenton & Bell 1981, O'Farrel *et al.* 1999, Russo & Jones 2002, Schnitzler *et al.* 2003, Walters *et al.* 2012). Several mechanisms of frequency segregation among sympatric and/or sister species have been proposed, including differences in body size (Heller & von Helversen 1989, Jones 1999), prey size preferences (Jones & van Parijs 1993, Houston *et al.* 2004, Safi & Siemers 2010), and intraspecific communication (Heller & von Helversen 1989, Thabah *et al.* 2006, Russo *et al.* 2007, Jones 2008, Jones & Siemers 2010).

Several studies disregard the trophic niche partitioning as a driver of echolocation frequency divergence, arguing that the differences in detection resolution between similar frequencies are negligible, and finding significant dietary

overlap (e.g. Kingston *et al.* 2001, Jones & Barlow 2004, Thabah *et al.* 2006, Jacobs *et al.* 2007, Russo *et al.* 2007, Jones & Siemers 2010). As well, intraspecific communication (see Jones 2008, Jones & Siemers 2010) not necessarily holds as the principal mechanism driving the maintenance of species-specific frequencies, given that the major purpose of echolocation – self-recognition of the emitted call (Obrist 1995, Barclay 1999) – is also facilitated by these call differences. Moreover, several species have social call repertoires different from the echolocation calls used for searching prey (e.g. Barclay *et al.* 1979, Barlow & Jones 1997, Pfalzer & Kusch 2003, Chaverri *et al.* 2010), and these social calls are more variable than echolocation ones (Fenton 1994). Bats may indeed be attracted by echolocating conspecifics, particularly those emitting feeding-buzzes (Gillam 2007, Cvikel *et al.* 2015a), but this attraction may elicit frequency alterations to avoid jamming (Ulanovsky *et al.* 2004, Gillam *et al.* 2007, Takahashi *et al.* 2014, but see Cvikel *et al.* 2015b), as well as antagonistic behaviors (Barlow & Jones 1997, Corcoran & Conner 2014).

The most consistent scaling of echolocation parameters is that with body size (Jones 1999). Both frequency (Aldridge & Rautenbach 1987, Norberg & Rayner 1987, Jakobsen *et al.* 2012) and time (Holderied & von Helversen 2003) parameters have a significant relationship with wing size and body mass, although there are known cases of deviations from this allometric scaling (Jacobs *et al.* 2007), as well as morphologically similar sister species with different echolocation frequencies (Jones & van Parijs 1993, Thabah *et al.* 2006). Nonetheless, this allometric scaling has been established without taking into account the phylogenetic relatedness among species (but see Jacobs *et al.* 2007, 2014), what can hamper its conclusions (Martins & Hansen 1997, Garland *et al.* 1999). Moreover, tonal calls comprise several spectral and temporal parameters, which serve different functions (Holderied & von Helversen 2003, Siemers & Schnitzler 2004), and thus may present disparate amounts of phylogenetic and spatial signals (McCracken & Sheldon 1997) as well as different relationships with morphological and environmental variables.

In this work we aim to investigate the magnitudes of the phylogenetic and spatial signals in the evolution of echolocation frequency and time parameters, and establish their relationships with morphological and environmental variables using

phylogenetically corrected regressions. Species often show similarities in structural and frequency parameters with those of its congeners (e.g. Taylor 1999, Russo & Jones 2002, see also Jones & Teeling 2006), so we can expect a relatively high amount of phylogenetic signal in some echolocation parameters. However, it is known that closely related species do differ in call bandwidth according to the habitats they forage in (Siemers & Schnitzler 2004), and whether the similarities in other call parameters among related species are due to habitat or phylogenetic structure is not thoroughly understood. We do not include the echolocating species from the family Pteropodidae because their echolocation is specialized and produced in a different way from laryngeal echolocation (Holland *et al.* 2004, Yovel *et al.* 2010, Boonman *et al.* 2014). We here intend to look into the macro-evolutionary and ecological grounds of tonal echolocation evolution, and hence we overlook the fine-scale alterations adopted by bats in specific situations (e.g. Brinkløv *et al.* 2010, Chiu *et al.* 2010, Bates *et al.* 2011, Falk *et al.* 2014) and the geographical intraspecific differences that are documented for some species (e.g. Guillen *et al.* 2000, Armstrong & Coles 2007, Chen *et al.* 2009, Veselka *et al.* 2013).

1.2 Material and Methods

1.2.1 Data collection:

We compiled echolocation parameters from published articles, theses, and field guides (see Table 1 for description of the studied parameters, and supplementary Table S1 for the references used for each species). Only calls explicitly measured during the search phase (Griffin *et al.* 1960) were used. The number of reported parameters varied considerably between sources, resulting in a final dataset with different levels of resolution for each parameter. Weighted averages were computed for each parameter, considering the sample size indicated in each source, and assuming a sample of just one individual when this information

was absent. We obtained wing measurement variables from 278 species at the Royal Ontario Museum mammal collection (29% of the echolocating bats based on Wilson & Reeder 2005. See Table S1 for a complete description of the dataset representativeness). Given that dried skins account for the majority of species in this collection, preventing the calculation of wing areas, we used two wing parameter indices proposed by Findley *et al.* (1972) (i.e. aspect ratio index and tip index; Table 2), as well as the forearm length. Additional forearm length information was obtained from the PanTHERIA dataset (Jones *et al.* 2009).

TABLE 1: Echolocation variables investigated in the present study. N corresponds to the available number of species for each parameter. See supplementary Table S2 for details on sample sizes and the parameters available for each species.

Parameter	**Description**	**N**
Peak frequency	The frequency with maximal amplitude (kHz)	262
Initial frequency	Starting pulse frequency (kHz)	240
Final frequency	Frequency at the end of the pulse (kHz)	243
Bandwidth	Difference between the initial and final frequencies (kHz)	251
Duration	Duration of the echolocation pulse (ms)	252

TABLE 2: Morphological and environmental variables used to model interspecific variation in echolocation acoustic parameters.

Parameter	**Description**
Forearm length	Length between the elbow and the wrist (mm)
Aspect ratio index	Length of (Digit III + Forearm) / Digit V
Tip index	Digit III / Forearm
NDVI	Normalized difference vegetation index
Bio01	Annual mean temperature
Bio04	Temperature seasonality
Bio28	Annual mean moisture index
Bio31	Moisture index seasonality

We combined geographical range maps obtained from the IUCN global mammal assessment (IUCN 2013) with four bioclimatic rasters from the CliMond

v1.1 dataset (Table 2; Kriticos *et al.* 2011) to estimate the average climatic conditions (environmental centroid) experienced by each species. Annual precipitation and precipitation seasonality were not included in further analyses due to their high correlation with mean annual moisture and moisture seasonality (r = 0.92 for both pairwise comparisons). We selected temperature and moisture variables because they are involved in atmospheric sound attenuation (Stilz & Schnitzler 2012), and the mean annual NDVI (FAO 2008) was selected to represent forest cover. The data extraction was performed using the `raster` 2.2-12 package (Hijmans 2014), in R 3.0.2 (R Core Team 2013). Phylogenetic information on the studied species was based on the 'best dates' supertree by Fritz *et al.* (2009). This tree is only 51% resolved, so we used 100 possible polytomy resolutions provided by Kuhn *et al.* (2011), considering them as equivalent to a Bayesian posterior distribution of trees. Fritz *et al.* tree represents an updated version of the Bininda-Emonds *et al.* (2007, 2008) supertree, after correcting some of the species names. We visually checked the bat nomenclature in the obtained tree, and found 60 additional incorrect species names, based on the Wilson and Reeder (2005) classification, the same used by the IUCN global mammal assessment. These names were corrected before the analyses, and the same nomenclature corrections were applied to Kuhn's *et al.* (2011) trees.

1.2.2 Analyses:

To determine the amount of phylogenetic and spatial autocorrelation in echolocation parameters, we used the method proposed by Freckleton & Jetz (2009) to estimate three parameters, namely ϕ, λ' and γ. ϕ measures the relative contribution of spatial and phylogenetic effects, and varies between zero (no spatial effect) and one (all the variation explained by the geographical distance). λ' is the spatially corrected version of Pagel's λ (Pagel 1999, hereafter λ_P), and is estimated as $(1 - \phi)\ \lambda_P$. Its definition follows the one proposed by Pagel (1999), varying from

zero (phylogenetic independence) to one (where trait values are structured according to a Brownian motion model of evolution). Finally, γ represents the trait variation independent of both phylogeny and space, defined as $(1 - \phi)(1 - \lambda_P)$. Thus, in this model, ϕ will be higher when trait similarities are due to the similar geographical distributions, and spatial effects have a preponderant influence on trait evolution. Conversely, λ' will be higher when close relatives are similar owing to their shared evolutionary history.

The method of Freckleton & Jetz (2009) also allows for the fitting of a linear model on the phylogenetic independent contrasts scaled by the geographic distances among observations, thus accounting for both phylogenetic and spatial dependencies (see also Diniz-Filho *et al.* 2007). We extended their method to perform stepwise model selection, based on the Akaike Information Criterion (AIC). A bidirectional approach was used, in which variables are sequentially removed from the global model, but can be added back in latter steps, mimicking a best subset selection approach (James *et al.* 2013). The three morphological and five environmental variables present in Table 2 composed the global model, also including quadratic terms for Bio01 and Bio28, as well as a multiplicative interaction between these variables. This model was evaluated for each phylogenetic resolution, and the variables excluded by the stepwise selection were sequentially removed from the model. In each step, the variable excluded by the majority of trees was omitted, and the resultant model was reevaluated until the recovery of a model supported by all possible phylogenies. To assess model adequacy, for each tree resolution we compared the final model selected through the stepwise process to a set of null models (Table 3), considering it satisfactory only if supported by all tree resolutions. All variables were transformed to z-scores prior to model fitting. The same global model was used to predict the variation in each echolocation parameter described in Table 1. Given that there is a broad spectrum of frequencies used by bats, the dependent variables were log transformed prior to the analyses. All analyses were conducted on R 3.0.2 (R Core

Team 2013), with the major packages `ape` 3.0-11 (Paradis *et al.* 2004) and `MASS` 7.3-29 (Venables & Ripley 2002).

TABLE 3: Models used to evaluate the variation in echolocation parameters and assess the importance of the phylogenetic and/or spatial components. The global model was subject to the stepwise variable selection (see text), while the four other models comprise the set of null models compared to the final one through AIC.

Model	**Parameters**	**λ'**	**ϕ**
Global model	All parameters described in Table 2	Estimated	Estimated
No coefficients	No parameters included	Estimated	Estimated
λ only	The final model selected for each echolocation variable	1.00	0.00
ϕ only	The final model selected for each echolocation variable	0.00	1.00
Independent	The final model selected for each echolocation variable	0.00	0.00

1.3 Results

Overall, echolocation call parameters show a greater proportion of phylogenetic signal over spatial signal (Table 4, Figure 1). Peak frequency, final frequency and call duration show the greatest amount of phylogenetic contribution, and the smallest spatial autocorrelation. Initial frequency has somewhat intermediate estimates of phylogenetic and spatial signals, with overlapping confidence intervals. Removing the species that produce constant frequency calls, in which the initial and peak frequencies are very close or identical, barely changes the estimated initial frequency spatial component ($\phi = 0.362$), and the phylogenetic component suffers just a minor reduction ($\lambda' = 0.432$). Frequency bandwidth, on the other hand, is the only parameter that shows a value of ϕ greater than that of λ'. This parameter also presents the highest independent component γ. The independent component reveals similar estimates of variation independent from

phylogeny and space for the peak, initial and final frequencies, and a lower estimate for call duration.

TABLE 4: Estimates of the relative contribution of the phylogenetic, spatial and independent components in the studied echolocation call parameters. Values represent the median and 95% confidence interval among 100 phylogenetic trees.

Parameter	**phylogenetic (λ')**	**spatial (ϕ)**	**independent (γ)**
Peak frequency	0.650 (0.55 – 0.75)	0.150 (0.01 – 0.30)	0.201 (0.13 – 0.27)
Initial frequency	0.443 (0.37 – 0.56)	0.365 (0.23 – 0.45)	0.196 (0.15 – 0.23)
Final frequency	0.724 (0.62 – 0.78)	0.057 (0.01 – 0.19)	0.220 (0.16 – 0.25)
Bandwidth	0.200 (0.14 – 0.27)	0.401 (0.24 – 0.50)	0.394 (0.32 – 0.49)
Duration	0.841 (0.80 – 0.87)	0.010 (0.01 – 0.06)	0.147 (0.11 – 0.17)

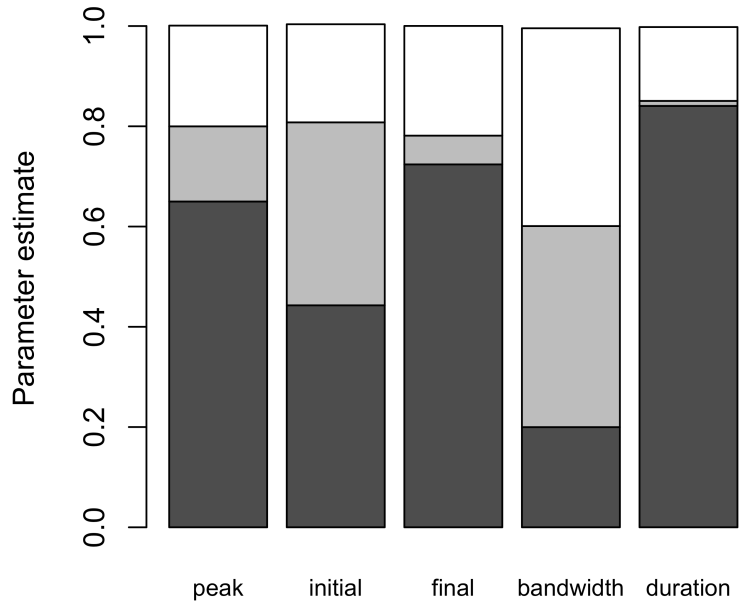


FIGURE 1: Bar charts showing the median values of λ' (dark grey), ϕ (light grey), and γ (white) components estimated for each echolocation call parameter.

Different models were selected for each studied characteristic, showing different relationships between morphological and environmental variables shaping

the variation in these parameters. Among the studied variables, only aspect ratio index was selected as an important variable for all echolocation parameters (Table 5). The results for all four frequency parameters show a consistent pattern of lower frequencies being produced by larger species, as well as those with greater aspect ratio indexes. Call duration, on the other hand, presents an inverse pattern with respect to those two variables.

Amongst environmental variables, annual mean temperature was selected for all call parameters except frequency bandwidth, presenting a pattern of higher frequencies, with low call duration, being produced in regions characterized by high average temperatures. Annual mean moisture was selected only in the models of initial frequency, also with a positive effect. Forest cover, on the other hand, has a negative influence on the initial frequency and a positive effect on call duration. Although frequency bandwidth presented the highest spatial autocorrelation, all environmental variables were discarded following stepwise selection.

TABLE 5: Model coefficients estimated for each echolocation call parameter. Values represent median and 95% confidence interval across phylogenetic tree resolutions. Blank spaces represent variables not included in the final model for the corresponding echolocation parameter. Note that values are in log-linear form.

Call parameter	**Aspect ratio index**	**Forearm length**	**Tip index**	**Bio01**	**Bio28**	**NDVI**
Peak	-0.130 (-0.15 -0.12)	-0.170 (-0.18 -0.16)	0.060 (0.05 0.07)	0.034 (0.03 0.04)		
Initial	-0.228 (-0.25 -0.21)	-0.148 (-0.15 -0.14)		0.046 (0.04 0.05)	0.111 (0.10 0.12)	-0.090 (-0.10 -0.07)
Final	-0.150 (-0.17 -0.14)	-0.196 (-0.20 -0.19)		0.061 (0.06 0.07)		
Bandwidth	-0.438 (-0.46 -0.41)		0.209 (0.19 0.23)			
Duration	0.285 (0.26 0.32)	0.180 (0.17 0.19)	-0.119 (-0.13 -0.10)	-0.103 (-0.11 -0.09)		0.075 (0.07 0.09)

Despite the reasonably high uncertainty in the estimates of the spatial parameter (ϕ) across trees, for all echolocation call parameters the final models

selected through the stepwise procedure had the smaller AIC value when compared to the considered null models. Even for the call duration parameter, where the median ϕ estimate appears at the lower boundary of this parameter, the model estimating λ' and fixing ϕ at zero was only the third best, with the one estimating both λ' and ϕ, with no variables, appearing as second best for most tree resolutions (Tables S2 to S6).

1.4 Discussion

According to our findings, the four frequency parameters reflect the interplay between environment and phylogenetic history in shaping the variation in echolocation calls. Among these, frequency bandwidth appears as the most plastic and environmentally structured trait, consistent with the background perception task played by the frequency spectrum (Siemers & Schnitzler 2004, Schmieder *et al.* 2012, Denzinger & Schnitzler 2013). The other three frequency parameters show similar estimates of the independent component γ, with peak frequency in between the more spatially structured initial frequency and the more phylogenetically structured final frequency. Call duration, on the other hand, shows the strongest phylogenetic structure, and the smallest independent component. This may be due to the coupling between pulse emission and wing beat in aerial hawking species (Speakman & Racey 1991, Denzinger *et al.* 2004), also shown through the regression coefficients, where the largest animals produce the longest calls (but see Jones 1999). Although the basic call structures are somewhat conserved within families (Jones & Teeling 2006), echolocation features are commonly linked to the habitat in which species forage and commute (Schnitzler & Kalko 2001, Schnitzler *et al.* 2003, Surlykke & Kalko 2008). There is ample variation in habitat use and foraging mode even within families (Denzinger & Schnitzler 2013), and the differences in phylogenetic and spatial signals between parameters show that some features are more adaptable than others in response to the environment.

Various different evolutionary processes and rates can generate similar patterns of phylogenetic signal (Revell *et al.* 2008), but some have stronger impacts than others towards decreasing its estimations, and thus can be disfavored by the results found herein. For example, processes of strong stabilizing selection, punctuated evolution and adaptive radiations may completely erase the signal (Hansen & Martins 1996, Revell *et al.* 2008, Kamilar & Cooper 2013). Behavioral characteristics also commonly bear very low to no phylogenetic autocorrelation (Blomberg *et al.* 2003, Tobias 2011, but see Kamilar & Cooper 2013), and thus the high phylogenetic signal found for most parameters may indicate that the communication role played by echolocation (e.g. Ruczyński *et al.* 2007, 2009) may not be preponderant in the evolution of the biosonar.

The frequency parameters show the expected relationship with body size, with larger animals producing lower frequency calls (Jones 1999, Jacobs *et al.* 2007, Jakobsen *et al.* 2013). Their relation with ambient temperature and moisture seems counterintuitive based on sound attenuation alone, given that higher frequencies are more severely attenuated in warmer and wetter conditions (Lawrence & Simmons 1982, Snell-Rood 2012, Luo *et al.* 2014). High frequencies are associated with the concentration of energy on the second harmonic (Guillen *et al.* 2000), a characteristic found in several species that inhabit the tropical region. Moreover, world's warmer and wetter environments tend to be associated with more dense vegetation (Chapin III *et al.* 2002), in which higher frequencies and broader bandwidths provide more details and directionality to differentiate food items from the surrounding clutter (Lawrence & Simmons 1982, Siemers & Schnitzler 2004, Stilz & Schnitzler 2012, Jakobsen *et al.* 2012, 2013, Denzinger & Schnitzler 2013). However, only the initial frequency showed a consistent relationship with NDVI among all frequency parameters, indicating lower initial frequencies in areas with denser vegetation. This result is consistent with the known positive correlation between wing area and habitat complexity (Fenton 1990, Safi & Dechmann 2005). Longer duration calls provide more information about the background clutter, despite narrowing the prey perception window (Denzinger & Schnitzler 2013), but the positive effect of NDVI on call duration is more probably a consequence of

narrowband callers that fly above the canopy in tropical regions, and thus are not affected by clutter (Griffin 1971, Jung *et al.* 2014).

Bats can dynamically adapt their acoustic beam shape through changes in amplitude and frequency (Surlykke *et al.* 2009, Jakobsen *et al.* 2012, 2013), and several species are known to use different frequencies across their geographic range (e.g. Macias & Mora 2003, Chen *et al.* 2009, Sun *et al.* 2013). These sources of intraspecific variation might weaken the results found herein (see Harmon & Losos 2005, Ives *et al.* 2007), but currently (to the best of our knowledge) there is no available method that estimates both phylogenetic and spatial autocorrelation simultaneously while accounting for intraspecific errors. For instance, estimating Pagel's lambda (λ_P) accounting for intraspecific errors (see Supplementary Material and Methods) resulted in phylogenetic signals higher than those estimated without intraspecific errors for all characters, with pairwise differences always lower than 0.0015. Given that the geographic centroids do not vary, the estimates of λ' and ϕ including standard errors would probably display a similar effect as found for λ_P, and these minor changes would barely alter the regression coefficients. Taxon sampling, on the other hand, is known to not significantly alter the estimates of phylogenetic signal or correlation coefficients (Ackerly 2000, Freckleton *et al.* 2002, Münkemüller *et al.* 2012), but its impact on the estimation of the spatial signal needs further investigation. Topological errors are another known source of bias in phylogenetic signal estimation, also tending to decrease the signal (Blomberg *et al.* 2003).

In conclusion, our study confirms several proposed relationships between morphology, environment and echolocation, but for the first time using phylogenetically corrected regressions in an analysis comprising all laryngeal echolocating families. Also, we show that the different components of the echolocation pulse have distinct phylogenetic and spatial signals, suggesting that these components play different roles in the environmental perception and food location. The overall preponderance of phylogenetic over the spatial signal does not argue against the role of habitat in shaping the variation in echolocation characteristics. While spatial autocorrelation is measured based on the geographical

distances among species distributions, habitat structuring of echolocation design is based on the distance to vegetation that a species commonly forage (Schnitzler & Kalko 2001, Surlykke & Kalko 2008). Close relatives tend to occupy similar habitats (Villalobos *et al.* 2013), and hence display a high phylogenetic signal even if the spatial autocorrelation was also high (Freckleton & Jetz 2009, Cooper *et al.* 2011). Further analyses are necessary to confirm if the relatively high phylogenetic signal found herein indeed dismiss the role of intraspecific communication in the evolution of echolocation. There is evidence that geographical alterations in echolocation parameters, being it for effective intraspecific communication or self-recognition, is a process that responds to local scale conditions and community composition (Heller & von Helversen 1989, Guillen *et al.* 2000, Russo *et al.* 2007, Sun *et al.* 2013), and in fact no one parameter analyzed can be totally explained by phylogenetic and spatial effects, evidencing this degree of ecological and behavioral plasticity.

1.5 References:

Ackerly, D.D. 2000. Taxon sampling, correlated evolution, and independent contrasts. *Evolution (N. Y).* **54**: 1480–1492.

Aldridge, H. & Rautenbach, I.L. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. *J. Anim. Ecol.* **56**: 763–778.

Armstrong, K.N. & Coles, R.B. 2007. Echolocation call frequency differences between geographical isolates of *Rhinonicteris aurantia* (Chiroptera: Hipposideridae): implications of nasal chamber size. *J. Mammal.* **88**: 94–104.

Barclay, R.M.R., Fenton, M.B. & Thomas, D.W. 1979. Social behavior of the little brown bat, *Myotis lucifugus*. *Behav. Ecol. Sociobiol.* **6**: 137–146.

Barlow, K.E. & Jones, G. 1997. Function of pipistrelle social calls: field data and a playback experiment. *Anim. Behav.* **53**: 991–999.

Bates, M.E., Simmons, J.A. & Zorikov, T. V. 2011. Bats Use Echo Harmonic Structure to Distinguish Their Targets from Background Clutter. *Science.* **333**: 627–630.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., *et al.* 2007. The delayed rise of present-day mammals. *Nature* **446**: 507–512.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., *et al.* 2008. The delayed rise of present-day mammals (corrigendum). *Nature* **456**: 274.

Blomberg, S.P. & Garland, T. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *J. Evol. Biol.* **15**: 899–910.

Blomberg, S.P., Garland, T. & Ives, A.R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution (N. Y).* **57**: 717–745.

Boonman, A., Bar-On, Y. & Yovel, Y. 2013. It's not black or white - on the range of vision and echolocation in echolocating bats. *Front. Physiol.* **4**.

Boonman, A., Bumrungsri, S. & Yovel, Y. 2014. Nonecholocating Fruit Bats Produce Biosonar Clicks with Their Wings. *Curr. Biol.* **24**: 2962–2967.

Brinkløv, S., Kalko, E. & Surlykke, A. 2010. Dynamic adjustment of biosonar intensity to habitat clutter in the bat *Macrophyllum macrophyllum* (Phyllostomidae). *Behav. Ecol. Sociobiol.* **64**: 1867–1874.

Chapin III, F.S., Matson, P.A. & Vitousek, P. 2011. *Principles of terrestrial ecosystem ecology*. Springer Science & Business Media.

Chaverri, G., Gillam, E.H. & Vonhof, M.J. 2010. Social calls used by a leaf-roosting bat to signal location. *Biol. Lett.* **6**: 441–444.

Chen, S.-F., Jones, G. & Rossiter, S.J. 2009. Determinants of echolocation call frequency variation in the Formosan lesser horseshoe bat (*Rhinolophus monoceros*). *Proc. R. Soc. B Biol. Sci.* **276**: 3901–3909.

Chiu, C., Reddy, P.V., Xian, W., Krishnaprasad, P.S. & Moss, C.F. 2010. Effects of competitive prey capture on flight behavior and sonar beam pattern in paired big brown bats, *Eptesicus fuscus*. *J Exp Biol* **213**: 3348–3356.

Cooper, N., Freckleton, R.P. & Jetz, W. 2011. Phylogenetic conservatism of environmental niches in mammals. *Proc. R. Soc. B Biol. Sci.*, doi: 10.1098/rspb.2010.2207.

Corcoran, A.J. & Conner, W.E. 2014. Bats jamming bats: Food competition through sonar interference. *Science.* **346**: 745–747.

Cvikel, N., Berg, K.E., Levin, E., Hurme, E., Borissov, I., Boonman, A., *et al.* 2015. Bats Aggregate to Improve Prey Search but Might Be Impaired when Their Density Becomes Too High. *Curr. Biol.* **25**: 205–211.

Cvikel, N., Levin, E., Hurme, E., Borissov, I., Boonman, A., Amichai, E., *et al.* 2015. On-board recordings reveal no jamming avoidance in wild bats. *Proc. R. Soc. B Biol. Sci.* **282**.

Denzinger, A., Kalko, E.K. V & Jones, G. 2004. Ecological and evolutionary aspects of echolocation in bats. In: *Echolocation in bats and dolphins* (J. Thomas, C. F. Moss, & M. Vater, eds), pp. 311–326. The University of Chicago Press.

Denzinger, A. & Schnitzler, H.-U. 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Front. Physiol.* **4**.

Diniz-Filho, J.A.F., Bini, L.M., Rodriguez, M.A., Rangel, T. & Hawkins, B.A. 2007. Seeing the forest for the trees: partitioning ecological and phylogenetic components of Bergmann's rule in European Carnivora. *Ecography (Cop.).* **30**: 598-608.

Falk, B., Jakobsen, L., Surlykke, A. & Moss, C.F. 2014. Bats coordinate sonar and flight behavior as they forage in open and cluttered environments. *J. Exp. Biol.* **217**: 4356–4364.

Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* **125**: 1–15.

Fenton, M.B. 1994. Assessing signal variability and reliability: "to thine ownself be true." *Anim. Behav.* **47**: 757–764.

Fenton, M.B. 1990. The foraging behaviour and ecology of animal-eating bats. *Can. J. Zool.* **68**: 411–422.

Fenton, M.B. & Bell, G.P. 1981. Recognition of species of insectivorous bats by their echolocation calls. *J. Mammal.* 233–243.

Findley, J.S., Studier, E.H. & Wilson, D.E. 1972. Morphologic properties of bat wings. *J. Mammal.* 429–444.

Freckleton, R.P., Harvey, P.H. & Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**: 712–726.

Freckleton, R.P. & Jetz, W. 2009. Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proc. R. Soc. B Biol. Sci.* **276**: 21–30.

Fritz, S.A., Bininda-Emonds, O.R.P. & Purvis, A. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* **12**: 538–549.

Garland, T., Midford, P.E. & Ives, A.R. 1999. An Introduction to Phylogenetically Based Statistical Methods, with a New Method for Confidence Intervals on Ancestral Values. *Am. Zool.* **39**: 374–388.

Gillam, E.H. 2007. Eavesdropping by bats on the feeding buzzes of conspecifics. *Can. J. Zool.* **85**: 795–801.

Gillam, E.H., Ulanovsky, N. & McCracken, G.F. 2007. Rapid jamming avoidance in biosonar. *Proc. R. Soc. B Biol. Sci.* **274**: 651–660.

Gould, E. 1988. Wing-clapping sounds of *Eonycteris spelaea* (Pteropodidae) in Malaysia. *J. Mammal.* **69**: 378–379.

Griffin, D.R. 1946. Supersonic cries of bats. *Nature* **158**: 46–48.

Griffin, D.R. 1971. The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). *Anim. Behav.* **19**: 55–61.

Griffin, D.R., Webster, F.A. & Michael, C.R. 1960. The echolocation of flying insects by bats. *Anim. Behav.* **8**: 141–154.

Guillén, A., Juste, B. & Ibáñez, C. 2000. Variation in the frequency of the echolocation calls of Hipposideros ruber in the Gulf of Guinea: an exploration of the adaptive meaning of the constant frequency value in rhinolophoid CF bats. *J. Evol. Biol.* **13**: 70–80.

Hansen, T.F. & Martins, E.P. 1996. Translating between microevolutionary process and macroevolutionary patterns: the correlation structure of interspecific data. *Evolution (N. Y).* **50**: 1404–1417.

Harmon, L.J. & Losos, J.B. 2005. The effect of intraspecific sample size on type I and type II error rates in comparative studies. *Evolution (N. Y).* **59**: 2705–2710.

Harvey, P.H. & Pagel, M.D. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford.

Heller, K.-G. & Helversen, O. v. 1989. Resource partitioning of sonar frequency bands in rhinolophoid bats. *Oecologia* **80**: 178–186.

Hijmans, R.J. 2014. raster: Geographic data analysis and modeling. R package version 2.3-12.

Holderied, M.W. & von Helversen, O. 2003. Echolocation range and wingbeat period match in aerial-hawking bats. *Proc. R. Soc. London. Ser. B Biol. Sci.* **270**: 2293–2299.

Holland, R.A., Waters, D.A. & Rayner, J.M. V. 2004. Echolocation signal structure in the Megachiropteran bat Rousettus aegyptiacus Geoffroy 1810. *J. Exp. Biol.* **207**: 4361–4369.

Houston, R.D., Boonman, A.M. & Jones, G. 2004. Do echolocation signal parameters restrict bats' choice of prey? In: *Echolocation in bats and dolphins* (J. A. Thomas, C. F. Moss, & M. Vater, eds), pp. 339–345. The University of Chicago Press.

IUCN. 2013. The IUCN red list of threatened species. Downloaded on 15 March 2014.

Ives, A.R., Midford, P.E. & Garland, T. 2007. Within-Species Variation and Measurement Error in Phylogenetic Comparative Methods. *Syst. Biol.* **56**: 252–270.

Jacobs, D., Barclay, R. & Walker, M. 2007. The allometry of echolocation call frequencies of insectivorous bats: why do some species deviate from the pattern? *Oecologia* **152**: 583–594.

Jacobs, D.S., Bastian, A. & Bam, L. 2014. The influence of feeding on the evolution of sensory signals: a comparative test of an evolutionary trade-off between masticatory and sensory functions of skulls in southern African Horseshoe bats (Rhinolophidae). *J. Evol. Biol.* **27**: 2829–2840.

Jakobsen, L., Brinkløv, S. & Surlykke, A. 2013. Intensity and directionality of bat echolocation signals. *Front. Physiol.* **4**.

Jakobsen, L., Ratcliffe, J.M. & Surlykke, A. 2012. Convergent acoustic field of view in echolocating bats. *Nature* **493**: 93–96.

James, G., Witten, D., Hastie, T. & Tibshirani, R. 2013. *An introduction to statistical learning*. Springer.

Jones, G. 1999. Scaling of echolocation call parameters in bats. *J Exp Biol* **202**: 3359–3367.

Jones, G. 2008. Sensory Ecology: Echolocation Calls Are Used for Communication. *Curr. Biol.* **18**: R34–R35.

Jones, G. & Barlow, K.E. 2004. Cryptic species of echolocating bats. In: *Echolocation in bats and dolphins* (J. A. Thomas, C. F. Moss, & M. Vater, eds), pp. 345–349. The University of Chicago Press.

Jones, G. & Holderied, M.W. 2007. Bat echolocation calls: adaptation and convergent evolution. *Proc. R. Soc. B Biol. Sci.* **274**: 905–912.

Jones, G. & Parijs, S.M. Van. 1993. Bimodal Echolocation in Pipistrelle Bats: Are Cryptic Species Present? *Proc. R. Soc. London. Ser. B Biol. Sci.* **251**: 119–125.

Jones, G. & Siemers, B. 2010. The communicative potential of bat echolocation pulses. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **197**: 447–457.

Jones, G. & Teeling, E.C. 2006. The evolution of echolocation in bats. *Trends Ecol. Evol.* **21**: 149–156.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., *et al.* 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**: 2648.

Jung, K., Molinari, J. & Kalko, E.K. V. 2014. Driving Factors for the Evolution of Species-Specific Echolocation Call Design in New World Free-Tailed Bats (Molossidae). *PLoS One* **9**: e85279.

Kamilar, J.M. & Cooper, N. 2013. Phylogenetic signal in primate behaviour, ecology and life history. *Philos. Trans. R. Soc. B Biol. Sci.* **368**.

Kingston, T., Lara, M.C., Jones, G., Akbar, Z., Kunz, T.H. & Schneider, C.J. 2001. Acoustic divergence in two cryptic Hipposideros species: a role for social selection? *Proc. R. Soc. London. Ser. B Biol. Sci.* **268**: 1381–1386.

Korine, C. & Kalko, E. 2005. Fruit detection and discrimination by small fruit-eating bats (Phyllostomidae): echolocation call design and olfaction. *Behav. Ecol. Sociobiol.* **59**: 12–23.

Kriticos, D.J., Webber, B.L., Leriche, A., Ota, N., Macadam, I., Bathols, J., *et al.* 2011. CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods Ecol. Evol.* **3**: 53–64.

Kuhn, T.S., Mooers, A.Ø. & Thomas, G.H. 2011. A simple polytomy resolver for dated phylogenies. *Methods Ecol. Evol.* **2**: 427–436.

Lawrence, B.D. & Simmons, J.A. 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J. Acoust. Soc. Am.* **71**: 585–590.

Lennon, J.J. 2000. Red-shifts and red herrings in geographical ecology. *Ecography (Cop.).* **23**: 101–113.

Luo, J., Koselj, K., Zsebők, S., Siemers, B.M. & Goerlitz, H.R. 2014. Global warming alters sound transmission: differential impact on the prey detection ability of echolocating bats. *J. R. Soc. Interface* **11**: 20130961.

Macías, S. & Mora, E.C. 2003. Variation of echolocation calls of *Pteronotus quadridens* (Chiroptera: Mormoopidae) in Cuba. *J. Mammal.* **84**: 1428–1436.

Martins, E.P. & Hansen, T.F. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am Nat* **149**: 646-667.

McCracken, K.G. & Sheldon, F.H. 1997. Avian vocalizations and phylogenetic signal. *Proc. Natl. Acad. Sci.* **94**: 3833–3836.

Moss, C.F. & Surlykke, A. 2010. Probing the Natural Scene by Echolocation in Bats. *Front. Behav. Neurosci.* **4**.

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., *et al.* 2012. How to measure and test phylogenetic signal. *Methods Ecol. Evol.* **3**: 743–756.

FAO. 2008. Global Pattern, Trends and Confidence Levels of Annual Sum NDVI (1981-2003). Downloaded on 13 Frebruary 2013.

Norberg, U.M. & Rayner, J.M. V. 1987. Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation. *Philos. Trans. R. Soc. London. B, Biol. Sci.* **316**: 335–427.

Nunn, C.L. 2011. *The comparative approach in evolutionary anthropology and biology*. University of Chicago Press.

O'Farrell, M.J., Miller, B.W. & Gannon, W.L. 1999. Qualitative identification of free-flying bats using the Anabat detector. *J. Mammal.* **80**: 11–23.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* **401**: 877–884.

Paradis, E., Claude, J. & Strimmer, K. 2004. APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics* **20**: 289–290.

Pfalzer, G. & Kusch, J. 2003. Structure and variability of bat social calls: implications for specificity and individual recognition. *J. Zool.* **261**: 21–33.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Revell, L.J. 2010. Phylogenetic signal and linear regression on species data. *Methods Ecol. Evol.* **1**: 319-329.

Revell, L.J., Harmon, L.J. & Collar, D.C. 2008. Phylogenetic signal, evolutionary process, and rate. *Syst. Biol.* **57**: 591-601.

Ruczyński, I., Kalko, E.K. V & Siemers, B.M. 2009. Calls in the Forest: A Comparative Approach to How Bats Find Tree Cavities. *Ethology* **115**: 167–177.

Ruczyński, I., Kalko, E.K. V & Siemers, B.M. 2007. The sensory basis of roost finding in a forest bat, *Nyctalus noctula*. *J. Exp. Biol.* **210**: 3607–3615.

Russo, D. & Jones, G. 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *J. Zool.* **258**: 91–103.

Russo, D., Mucedda, M., Bello, M., Biscardi, S., Pidinchedda, E. & Jones, G. 2007. Divergent echolocation call frequencies in insular rhinolophids (Chiroptera): a case of character displacement? *J. Biogeogr.* **34**: 2129–2138.

Safi, K. & Dechmann, D.K.N. 2005. Adaptation of brain regions to habitat complexity: a comparative analysis in bats (Chiroptera). *Proc. R. Soc. B Biol. Sci.* **272**: 179–186.

Safi, K. & Siemers, B. 2010. Implications of sensory ecology for species coexistence: biased perception links predator diversity to prey size distribution. *Evol. Ecol.* **24**: 703–713.

Schmieder, D.A., Kingston, T., Hashim, R. & Siemers, B.M. 2012. Sensory constraints on prey detection performance in an ensemble of vespertilionid understorey rain forest bats. *Funct. Ecol.* **26**: 1043–1053.

Schnitzler, H.-U., Moss, C.F. & Denzinger, A. 2003. From spatial orientation to food acquisition in echolocating bats. *Trends Ecol. Evol.* **18**: 386–394.

Schnitzler, H.U. & Kalko, E.K. V. 2001. Echolocation by insect-eating bats. *Bioscience* **51**: 557–569.

Schuller, G. & Moss, C.F. 2004. Vocal control and acoustically guided behavior in bats. In: *Echolocation in bats and dolphins* (J. Thomas, C. F. Moss, & M. Vater, eds), pp. 3–16. The University of Chicago Press.

Siemers, B.M. & Schnitzler, H.-U. 2004. Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature* **429**: 657–661.

Simmons, N.B. 2005a. An Eocene Big Bang for Bats. *Science.* **307**: 527–528.

Simmons, N.B. 2005b. Order Chiroptera. In: *Mammal Species of the World: a taxonomic and geographic reference* (D. E. Wilson & D. M. Reeder, eds), pp. 312–529. Johns Hopkins University Press.

Snell-Rood, E.C. 2012. The effect of climate on acoustic signals: Does atmospheric sound absorption matter for bird song and bat echolocation? *J. Acoust. Soc. Am.* **131**: 1650–1658.

Speakman, J.R. & Racey, P.A. 1991. No cost of echolocation for bats in flight. *Nature* **350**: 421–423.

Stilz, W.-P. & Schnitzler, H.-U. 2012. Estimation of the acoustic range of bat echolocation for extended targets. *J. Acoust. Soc. Am.* **132**: 1765–1775.

Sun, K., Luo, L., Kimball, R.T., Wei, X., Jin, L., Jiang, T., *et al.* 2013. Geographic Variation in the Acoustic Traits of Greater Horseshoe Bats: Testing the Importance of Drift and Ecological Selection in Evolutionary Processes. *PLoS One* **8**: e70368.

Surlykke, A., Boel Pedersen, S. & Jakobsen, L. 2009. Echolocating bats emit a highly directional sonar sound beam in the field. *Proc. R. Soc. B Biol. Sci.* **276**: 853–860.

Surlykke, A. & Kalko, E.K. V. 2008. Echolocating Bats Cry Out Loud to Detect Their Prey. *PLoS One* **3**: e2036.

Takahashi, E., Hyomoto, K., Riquimaroux, H., Watanabe, Y., Ohta, T. & Hiryu, S. 2014. Adaptive changes in echolocation sounds by *Pipistrellus abramus* in response to artificial jamming sounds. *J. Exp. Biol.* **217**: 2885–2891.

Teeling, E.C., Springer, M.S., Madsen, O., Bates, P., O'Brien, S.J. & Murphy, W.J. 2005. A Molecular Phylogeny for Bats Illuminates Biogeography and the Fossil Record. *Science.* **307**: 580–584.

Thabah, A., Rossiter, S.J., Kingston, T., Zhang, S., Parsons, S., Mya, K.M.Y.A., *et al.* 2006. Genetic divergence and echolocation call frequency in cryptic species of *Hipposideros larvatus* s.l. (Chiroptera: Hipposideridae) from the Indo-Malayan region. *Biol. J. Linn. Soc.* **88**: 119–130.

Tobias, M.L. 2011. Evolution of advertisement calls in African clawed frogs. *Behaviour* **148**: 519–549.

Ulanovsky, N., Fenton, M.B., Tsoar, A. & Korine, C. 2004. Dynamics of jamming avoidance in echolocating bats. *Proc. R. Soc. London. Ser. B Biol. Sci.* **271**: 1467–1475.

Venables, W.N. & Ripley, B.D. 2002. *Modern applied statistics with S*. Springer Science & Business Media.

Veselka, N., McGuire, L.P., Dzal, Y.A., Hooton, L.A. & Fenton, M.B. 2013. Spatial variation in the echolocation calls of the little brown bat (*Myotis lucifugus*). *Can. J. Zool.* **91**: 795–801.

Villalobos, F., Rangel, T.F. & Diniz-Filho, J.A.F. 2013. Phylogenetic fields of species: cross-species patterns of phylogenetic structure and geographical coexistence. *Proc. R. Soc. B Biol. Sci.* **280**.

Walters, C.L., Freeman, R., Collen, A., Dietz, C., Brock Fenton, M., Jones, G., *et al.* 2012. A continental-scale tool for acoustic identification of European bats. *J. Appl. Ecol.* **49**: 1064–1074.

Wilson, D.E. & Reeder, D.M. 2005. *Mammal species of the world. A taxonomic ang geographic reference*, 3rd ed. (D. E. Wilson & D. M. Reeder, eds). Johns Hopkins University Press.

Yovel, Y., Falk, B., Moss, C.F. & Ulanovsky, N. 2010. Optimal Localization by Pointing Off Axis. *Science.* **327**: 701–704.

1.6 Supplementary material

Supplementary Material and Methods

Pagel's lambda was estimated across trees with the function `phylosig` from the package `phytools` 0.3-72 (Revell 2012), with and without including the intraspecific standard errors. For each parameter we calculated the mean pairwise difference between the phylogenetic signal estimates across trees.

Revell, L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**: 217–223.

Table S1: Echolocation parameters available for each species included in the analyses and the respective data sources. Abbreviations refer to: peak frequency (PF), initial frequency (IF), final frequency (FF), bandwidth (BWD) and duration (D). N calls is the combined sample size between studies for each species. References are numbered according to the supplementary references.

Species	PF	IF	FF	BWD	D	N calls	References
Craseonycteris thonglongyai	PF			BWD	D	27	46, 130
Balantiopteryx io	PF	IF	FF	BWD	D	18	49
Balantiopteryx plicata	PF	IF	FF	BWD	D	155	49
Cormura brevirostris	PF	IF	FF	BWD	D	327	33, 59
Cyttarops alecto	PF	IF	FF	BWD	D	123	59
Emballonura monticola	PF	IF	FF	BWD	D	40	108
Peropteryx kappleri	PF	IF	FF	BWD	D	140	59
Peropteryx macrotis	PF	IF	FF	BWD	D	373	9, 15, 79, 115
Rhynchonycteris naso	PF	IF	FF	BWD	D	78	32, 93, 106
Saccolaimus saccolaimus	PF	IF	FF	BWD	D	198	108
Saccopteryx bilineata	PF	IF	FF	BWD	D	479	9, 59, 77, 79, 93, 106
Saccopteryx leptura	PF	IF	FF	BWD	D	329	9, 59, 106
Taphozous georgianus	PF	IF	FF	BWD	D	60	83
Taphozous hildegardeae		IF	FF			1	96
Taphozous mauritianus	PF	IF	FF	BWD	D	34	27, 86, 121, 131
Taphozous melanopogon	PF	IF	FF	BWD	D	120	108, 136
Taphozous nudiventris	PF	IF	FF	BWD	D	17	8
Taphozous perforatus	PF	IF	FF	BWD	D	94	7, 8, 33
Furipterus horrens		IF	FF	BWD		1	34, 107
Asellia tridens	PF	IF	FF	BWD	D	38	7, 56
Aselliscus stoliczkanus	PF	IF	FF	BWD	D	16	70, 138
Cloeotis percivali	PF	IF	FF	BWD	D	141	84, 86, 121, 131, 138
Coelops frithii	PF	IF	FF	BWD		21	138
Hipposideros armiger	PF	IF	FF	BWD	D	60	48, 105, 138, 141
Hipposideros ater	PF		FF	BWD	D	54	36
Hipposideros bicolor	PF					56	48, 65, 22
Hipposideros caffer	PF	IF	FF	BWD	D	122	84, 86, 121, 131
Hipposideros cervinus	PF					49	65
Hipposideros cineraceus	PF	IF	FF	BWD	D	117	21, 48, 65, 105
Hipposideros commersoni	PF	IF	FF	BWD	D	153	66
Hipposideros cyclops	PF					1	19
Hipposideros diadema	PF	IF	FF	BWD	D	32	42, 48, 82
Hipposideros fulvus	PF					1	65
Hipposideros galeritus	PF	IF	FF	BWD	D	28	48, 105
Hipposideros larvatus	PF	IF	FF	BWD	D	274	48, 105, 127, 134, 141
Hipposideros lylei	PF	IF	FF	BWD		3	127
Hipposideros pomona	PF	IF	FF	BWD	D	159	22, 105, 127
Hipposideros ruber	PF	IF	FF	BWD	D	449	28, 43, 86
Hipposideros speoris	PF			BWD	D	23	103
Hipposideros turpis	PF					45	48
Rhinonicteris aurantia	PF					158	1
Triaenops furculus	PF	IF	FF	BWD	D	153	3, 66
Triaenops persicus	PF	IF	FF	BWD	D	15	86
Cardioderma cor	PF					2	18
Megaderma lyra	PF	IF	FF	BWD	D	36	105, 111
Megaderma spasma	PF	IF	FF	BWD	D	4	105
Miniopterus fraterculus	PF	IF	FF	BWD	D	24	81, 86, 121
Miniopterus inflatus	PF	IF	FF	BWD	D	7	86
Miniopterus manavi	PF	IF	FF	BWD	D	77	66, 110
Miniopterus natalensis	PF	IF	FF	BWD	D	27	81, 86, 121
Miniopterus schreibersii	PF	IF	FF	BWD	D	279	95, 99, 114, 120
Cheiromeles torquatus	PF	IF	FF	BWD	D	84	64
Cynomops planirostris	PF	IF	FF	BWD	D	46	60

Eumops auripendulus	PF	IF	FF	BWD	D	41	60
Eumops bonariensis	PF	IF	FF	BWD	D	8	60
Eumops glaucinus	PF	IF	FF	BWD	D	306	60, 89
Eumops perotis	PF	IF	FF	BWD	D	50	2
Eumops underwoodi	PF	IF	FF	BWD	D	6	97
Molossops mattogrossensis	PF	IF	FF	BWD	D	24	60
Molossops neglectus	PF	IF	FF	BWD	D	28	60
Molossops temminckii	PF	IF	FF	BWD	D	127	44, 60
Molossus molossus	PF	IF	FF	BWD	D	216	15, 60, 94, 106
Molossus rufus	PF	IF	FF	BWD	D	333	15, 31, 33, 60, 79, 94
Molossus sinaloae	PF	IF	FF	BWD	D	203	15, 60, 79, 94, 97
Mormopterus loriae	PF					2	82
Mormopterus minutus	PF	IF	FF	BWD	D	24	88
Mormopterus planiceps	PF	IF	FF	BWD	D	20	37
Nyctinomops laticaudatus	PF	IF	FF	BWD	D	84	15, 60, 79
Nyctinomops macrotis	PF	IF	FF	BWD	D	481	2, 9, 60, 89
Otomops martiensseni	PF	IF	FF	BWD	D	62	29, 121
Promops centralis	PF	IF	FF	BWD	D	12	60
Promops nasutus	PF	IF	FF	BWD	D	30	60
Sauromys petrophilus	PF			BWD	D	61	120, 121
Tadarida aegyptiaca	PF	IF	FF	BWD	D	66	29, 120, 121, 131
Tadarida ansorgei	PF	IF	FF	BWD	D	4	84, 131
Tadarida brasiliensis	PF	IF	FF	BWD	D	350	2, 9, 60, 80, 91, 97, 113
Tadarida chapini	PF	IF	FF	BWD	D	1	131
Tadarida condylura	PF	IF	FF	BWD	D	37	30, 86, 121, 131
Tadarida fulminans	PF	IF	FF	BWD	D	1	27
Tadarida midas		IF	FF	BWD	D	23	30
Tadarida mops	PF	IF	FF	BWD	D	11	64
Tadarida nigeriae		IF	FF	BWD	D	19	30
Tadarida niveiventer	PF			BWD	D	6	121
Tadarida pumila	PF	IF	FF	BWD	D	116	29, 30, 86, 121, 131
Mormoops blainvillei	PF	IF	FF	BWD	D	181	55, 74
Mormoops megalophylla	PF	IF	FF	BWD	D	1503	15, 79, 97, 124
Pteronotus davyi	PF	IF	FF	BWD	D	1921	9, 15, 55, 79, 93, 97, 115, 124
Pteronotus gymnonotus	PF	IF	FF	BWD	D	11	50
Pteronotus macleayii	PF	IF	FF	BWD	D	171	74
Pteronotus parnellii	PF	IF	FF	BWD	D	1848	15, 55, 74, 79, 93, 97, 115, 124
Pteronotus personatus	PF	IF	FF	BWD	D	1147	15, 77, 79, 92, 96, 124
Pteronotus quadridens	PF	IF	FF	BWD	D	177	55, 74
Mystacina tuberculata	PF	IF	FF	BWD	D	235	57, 100, 101
Natalus stramineus	PF	IF	FF	BWD	D	17	55, 115
Nyctiellus lepidus	PF	IF	FF	BWD	D	28	91
Noctilio albiventris	PF	IF	FF	BWD	D	3	47, 62
Noctilio leporinus	PF	IF	FF	BWD	D	139	15, 94, 119
Nycteris grandis	PF	IF	FF	BWD	D	34	45, 131
Nycteris macrotis	PF	IF	FF	BWD	D	102	28, 121
Nycteris thebaica	PF	IF	FF	BWD	D	21	84, 120, 121, 131
Nycteris tragata	PF	IF	FF	BWD	D	30	108
Nycteris woodi	PF	IF	FF	BWD	D	1	131
Artibeus cinereus	PF	IF	FF	BWD	D	11	106
Artibeus jamaicensis	PF	IF	FF	BWD	D	101	55, 80, 87, 106
Artibeus lituratus	PF	IF	FF	BWD	D	20	106
Artibeus watsoni	PF	IF	FF	BWD	D	8	41, 67
Brachyphylla cavernarum	PF	IF	FF	BWD	D	4	55
Brachyphylla nana	PF	IF	FF	BWD	D	13	75
Carollia castanea		IF	FF	BWD	D	80	135
Carollia perspicillata	PF	IF	FF	BWD	D	650	12, 106, 135
Centurio senex		IF	FF	BWD	D	1	42
Chiroderma trinitatum	PF	IF	FF	BWD	D	3	106
Chiroderma villosum	PF	IF	FF	BWD	D	4	106
Choeroniscus minor	PF	IF	FF	BWD	D	5	106

Diaemus youngi	PF					1	16
Erophylla bombifrons	PF	IF	FF	BWD	D	5	55
Erophylla sezekorni	PF	IF	FF	BWD	D	11	91
Glossophaga longirostris	PF	IF	FF	BWD	D	8	55
Glossophaga soricina	PF	IF	FF	BWD	D	27	106
Lampronycteris brachyotis	PF	IF	FF	BWD	D	6	106
Macrophyllum macrophyllum	PF	IF	FF	BWD	D	1012	13, 14, 137
Macrotus californicus		IF	FF	BWD	D	1	6
Macrotus waterhousii	PF	IF	FF	BWD	D	16	91
Micronycteris hirsuta	PF	IF	FF	BWD	D	6	106
Micronycteris megalotis	PF	IF	FF	BWD	D	7	34, 106
Micronycteris minuta	PF	IF	FF	BWD	D	3	106
Mimon bennettii		IF	FF	BWD	D	1	34
Mimon crenulatum	PF	IF	FF	BWD	D	3	106
Monophyllus plethodon	PF	IF	FF	BWD	D	13	55, 80
Phyllonycteris poeyi	PF	IF	FF	BWD	D	88	87
Phyllops falcatus	PF	IF	FF	BWD	D	671	76, 87
Phyllostomus discolor		IF	FF	BWD		1	69
Phyllostomus hastatus	PF	IF	FF	BWD	D	4	61, 106
Platyrrhinus helleri	PF	IF	FF	BWD	D	5	106
Stenoderma rufum	PF	IF	FF	BWD	D	1	55
Sturnira lilium	PF	IF	FF	BWD	D	7	55
Sturnira tildae	PF	IF	FF	BWD	D	5	106
Tonatia saurophila	PF	IF	FF	BWD	D	6	106
Trachops cirrhosus	PF	IF	FF	BWD	D	22	5, 42, 129
Trinycteris nicefori	PF	IF	FF	BWD	D	2	106
Uroderma bilobatum	PF	IF	FF	BWD	D	9	106
Vampyressa pusilla		IF	FF	BWD	D	6	67
Vampyrum spectrum	PF	IF	FF	BWD	D	1	106
Rhinolophus acuminatus	PF					13	48, 65
Rhinolophus affinis	PF	IF	FF	BWD	D	118	48, 65, 105
Rhinolophus alcyone	PF					1	26
Rhinolophus arcuatus	PF					36	122
Rhinolophus beddomei	PF	IF	FF	BWD	D	1	125
Rhinolophus blasii	PF	IF	FF	BWD	D	45	8, 52, 86, 99, 121
Rhinolophus clivosus	PF	IF	FF	BWD	D	91	8, 52, 86, 120, 121
Rhinolophus darlingi	PF	IF	FF	BWD	D	24	52, 86, 121
Rhinolophus deckenii	PF	IF	FF	BWD	D	4	85, 86
Rhinolophus denti	PF				D	20	52, 121
Rhinolophus euryale	PF	IF	FF	BWD	D	103	99, 114, 116
Rhinolophus ferrumequinum	PF	IF	FF	BWD	D	467	8, 35, 39, 72, 95, 99, 102, 112, 114, 128
Rhinolophus fumigatus	PF				D	5	52, 85, 121
Rhinolophus hildebrandti	PF	IF	FF	BWD	D	26	52, 65, 86, 121
Rhinolophus hipposideros	PF	IF	FF	BWD	D	216	7, 65, 95, 99, 102, 112, 114
Rhinolophus landeri	PF	IF	FF	BWD	D	107	26, 28, 52, 65, 85, 121
Rhinolophus lepidus	PF				D	354	48, 65, 108
Rhinolophus luctus	PF				D	39	48, 65, 108, 138
Rhinolophus macrotis	PF					1	65
Rhinolophus malayanus	PF	IF	FF	BWD	D	245	48, 65, 105, 125
Rhinolophus megaphyllus	PF			BWD	D	29	36
Rhinolophus paradoxolophus	PF					1	24, 138
Rhinolophus pearsonii	PF					10	48, 65
Rhinolophus pusillus	PF	IF	FF	BWD	D	61	48, 65, 105, 138
Rhinolophus rouxii	PF				D	1385	92
Rhinolophus sedulus	PF					9	65
Rhinolophus shameli	PF	IF	FF	BWD	D	121	48, 51, 105
Rhinolophus simulator	PF	IF	FF	BWD	D	26	52, 86, 121
Rhinolophus sinicus	PF					67	138
Rhinolophus stheno	PF					137	48, 65, 125, 138
Rhinolophus trifoliatus	PF				D	77	48, 65, 108
Rhinopoma hardwickii	PF	IF	FF	BWD	D	107	33

Rhinopoma microphyllum	PF	IF	FF	BWD	D	10	8, 20
Thyroptera tricolor	PF		FF		D	61	32
Antrozous pallidus	PF	IF	FF	BWD	D	5	27
Barbastella barbastellus	PF	IF	FF	BWD	D	198	95, 102, 112, 114
Chalinolobus gouldii	PF	IF	FF	BWD	D	21	37, 38
Chalinolobus morio	PF	IF	FF	BWD	D	20	37
Chalinolobus picatus	PF					9	104
Chalinolobus tuberculatus	PF	IF	FF	BWD	D	381	100, 101
Corynorhinus townsendii		IF	FF	BWD	D	2	42, 68
Eptesicus brasiliensis	PF	IF	FF	BWD	D	2	106
Eptesicus furinalis	PF	IF	FF	BWD	D	318	79, 94, 115
Eptesicus fuscus	PF	IF	FF	BWD	D	1977	2, 15, 23, 33, 87, 90
Eptesicus hottentotus	PF			BWD	D	16	120, 121
Eptesicus nilssonii	PF	IF	FF	BWD	D	122	35, 95
Eptesicus serotinus	PF	IF	FF	BWD	D	252	95, 99, 102, 112, 114
Glauconycteris variegata	PF			BWD	D	1	121
Hesperoptenus blanfordi	PF	IF	FF	BWD	D	32	64, 105
Histiotus montanus	PF	IF	FF	BWD	D	56	113
Histiotus velatus		IF	FF	BWD	D	1	34, 107
Ia io	PF	IF	FF	BWD	D	4	133
Kerivoula argentata		IF	FF	BWD	D	1	27
Kerivoula lanosa	PF	IF	FF	BWD	D	7	86
Kerivoula papillosa	PF	IF	FF	BWD	D	218	63, 118
Kerivoula pellucida	PF	IF	FF	BWD	D	110	63, 118
Kerivoula picta	PF	IF	FF	BWD	D	271	126
Laephotis angolensis	PF	IF	FF	BWD	D	4	27
Laephotis wintoni	PF		FF	BWD	D	10	54, 121
Lasionycteris noctivagans	PF	IF	FF	BWD	D	678	4, 23, 94
Lasiurus blossevillii	PF	IF	FF	BWD	D	9	15, 58
Lasiurus borealis	PF	IF	FF	BWD	D	1082	17, 23, 90, 91
Lasiurus cinereus	PF	IF	FF	BWD	D	591	4, 23, 38, 94
Lasiurus ega	PF	IF	FF	BWD	D	267	58, 79, 94, 115
Lasiurus intermedius	PF	IF	FF	BWD	D	52	15, 79, 115
Murina aenea	PF	IF	FF	BWD	D	12	63
Murina cyclotis	PF	IF	FF	BWD	D	136	63, 118
Murina leucogaster	PF	IF	FF	BWD	D	190	35, 39, 72, 128
Murina suilla	PF	IF	FF	BWD	D	123	63, 118
Myotis adversus	PF	IF	FF	BWD	D	245	38, 108, 123
Myotis albescens	PF	IF	FF	BWD		1	11
Myotis auriculus	PF	IF	FF	BWD	D	1	123
Myotis austroriparius	PF	IF	FF	BWD	D	486	17
Myotis blythii	PF	IF	FF	BWD	D	201	95, 99, 114
Myotis bocagii	PF	IF	FF	BWD	D	7	86, 121
Myotis californicus	PF	IF	FF	BWD	D	904	40, 94, 123
Myotis chiloensis	PF	IF	FF	BWD	D	67	98, 113
Myotis ciliolabrum	PF	IF	FF	BWD	D	1104	40, 94
Myotis daubentonii	PF	IF	FF	BWD	D	253	95, 99, 102, 112, 114, 117, 128
Myotis evotis	PF	IF	FF	BWD	D	1	42
Myotis frater	PF	IF	FF	BWD	D	20	141
Myotis goudoti	PF	IF	FF	BWD	D	60	66
Myotis grisescens	PF	IF	FF	BWD	D	1588	17, 90
Myotis ikonnikovi	PF	IF	FF	BWD	D	41	35, 128
Myotis keaysi	PF	IF	FF	BWD	D	236	79, 112
Myotis leibii	PF	IF	FF	BWD	D	503	17, 90, 123
Myotis lucifugus	PF	IF	FF	BWD	D	3239	17, 23, 28, 90, 123
Myotis macrodactylus	PF	IF	FF	BWD	D	29	35, 39
Myotis muricola	PF	IF	FF	BWD	D	180	108
Myotis myotis	PF	IF	FF	BWD	D	189	95, 99, 114
Myotis mystacinus	PF	IF	FF	BWD	D	188	95, 99, 102, 112, 114, 123
Myotis nattereri	PF	IF	FF	BWD	D	335	8, 39, 95, 102, 112,114, 123
Myotis nigricans	PF	IF	FF	BWD	D	867	58, 106, 123

Myotis riparius	PF	IF	FF	BWD	D	33	32
Myotis ruber		IF	FF	BWD	D	1	123
Myotis septentrionalis	PF	IF	FF	BWD	D	1555	17, 23, 90
Myotis siligorensis	PF			BWD	D	28	130
Myotis sodalis	PF	IF	FF	BWD	D	2846	17, 90
Myotis thysanodes	PF	IF	FF	BWD	D	1	123
Myotis tricolor	PF	IF	FF	BWD	D	25	86, 120, 121, 131
Myotis velifer	PF	IF	FF	BWD	D	41	97
Myotis vivesi		IF	FF	BWD	D	1	10
Myotis volans	PF	IF	FF	BWD	D	2	123
Myotis welwitschii	PF			BWD	D	1	121
Myotis yumanensis	PF	IF	FF	BWD	D	338	94, 97
Nyctalus noctula	PF	IF	FF	BWD	D	398	25, 95, 99, 102, 112, 114
Nycticeinops schlieffeni	PF	IF	FF	BWD	D	33	30, 86, 121
Nycticeius humeralis	PF	IF	FF	BWD	D	298	17, 90
Nyctophilus geoffroyi	PF	IF	FF	BWD	D	21	37, 38
Nyctophilus timoriensis		IF	FF	BWD		16	104
Phoniscus jagorii	PF	IF	FF	BWD	D	20	63, 118
Pipistrellus abramus	PF	IF	FF	BWD	D	210	99, 71
Pipistrellus ariel	PF	IF	FF	BWD	D	290	7, 8
Pipistrellus hesperus	PF	IF	FF	BWD	D	1	42
Pipistrellus kuhlii	PF	IF	FF	BWD	D	314	8, 95, 99, 114
Pipistrellus nanus	PF	IF	FF	BWD	D	137	28, 30, 131
Pipistrellus pipistrellus	PF	IF	FF	BWD	D	362	8, 95, 99, 102, 112, 114, 117
Pipistrellus rueppellii	PF	IF	FF	BWD	D	1	27
Pipistrellus rusticus	PF	IF	FF	BWD	D	48	30, 121, 131
Pipistrellus savii	PF	IF	FF	BWD	D	162	95, 99, 114
Pipistrellus stenopterus	PF	IF	FF	BWD	D	44	64
Pipistrellus subflavus	PF	IF	FF	BWD	D	2514	17, 23, 73, 90
Plecotus auritus	PF	IF	FF	BWD	D	160	95, 112, 114
Plecotus austriacus	PF	IF	FF	BWD	D	393	95, 99, 109, 114, 132
Rhogeessa aeneus	PF	IF	FF	BWD	D	35	79, 115
Rhogeessa io	PF	IF	FF	BWD	D	4	106
Scotoecus albofuscus	PF			BWD	D	1	121
Scotophilus dinganii	PF	IF	FF	BWD	D	52	53, 86, 121
Scotophilus kuhlii	PF	IF	FF	BWD	D	270	108
Scotophilus nigrita	PF	IF	FF	BWD	D	2	27
Scotophilus viridis	PF	IF	FF	BWD	D	29	30, 86
Tylonycteris pachypus	PF	IF	FF	BWD	D	3874	105, 139, 140
Tylonycteris robustula	PF	IF	FF	BWD	D	1976	108, 139, 140
Vespadelus regulus	PF	IF	FF	BWD	D	20	37
Vespertilio sinensis	PF	IF	FF	BWD	D	41	35, 39

Table S2: ΔAIC between the final model (Global model) and the null models fitted to peak frequency on each phylogenetic tree. See Table 3 in the main text for the description of the null models.

Tree	Global model	No coefficients	λ only	ϕ only	Independent
1	0	84.25	92.25	186.29	151.28
2	0	108.00	116.00	207.46	151.18
3	0	147.95	155.95	202.45	149.25
4	0	93.48	101.48	198.52	147.82
5	0	157.58	165.58	198.04	150.75
6	0	235.16	243.16	191.23	137.86
7	0	63.96	71.96	256.22	142.21
8	0	368.85	376.85	203.33	148.20
9	0	272.24	280.24	214.10	145.22
10	0	134.04	142.04	226.60	146.14
11	0	116.59	124.59	222.29	138.17
12	0	196.50	204.50	237.66	148.58
13	0	179.39	187.39	195.93	142.58
14	0	84.78	92.78	193.90	147.07
15	0	149.67	157.67	191.80	146.19
16	0	110.97	118.97	175.87	148.31
17	0	112.89	120.89	183.00	144.67
18	0	118.05	126.05	184.03	142.94
19	0	146.22	154.22	211.43	152.21
20	0	132.81	140.81	196.10	145.01
21	0	128.37	136.37	200.63	147.91
22	0	130.01	138.01	240.90	144.51
23	0	145.23	153.23	231.75	146.71
24	0	135.09	143.09	238.19	144.00
25	0	61.58	69.58	306.91	147.79
26	0	144.42	152.42	226.87	142.28
27	0	213.80	221.80	231.40	142.56
28	0	199.97	207.97	167.92	150.86
29	0	101.68	109.68	183.71	149.39
30	0	134.77	142.77	210.85	146.14
31	0	179.65	187.65	200.35	151.05
32	0	143.83	151.83	192.98	146.16
33	0	145.26	153.26	168.45	145.86
34	0	228.22	236.22	222.94	143.90
35	0	305.59	313.59	223.86	147.77
36	0	116.78	124.78	225.19	142.23
37	0	147.03	155.03	186.67	144.73
38	0	96.79	104.79	179.96	147.70
39	0	110.33	118.33	214.84	139.52
40	0	87.12	95.12	225.98	145.23
41	0	115.46	123.46	182.87	152.12
42	0	125.99	133.99	184.76	143.82
43	0	135.94	143.94	202.28	145.20
44	0	90.42	98.42	215.39	144.81
45	0	247.58	255.58	170.03	146.36
46	0	127.97	135.97	248.71	151.80
47	0	125.78	133.78	259.52	142.71
48	0	108.55	116.55	299.02	147.40
49	0	80.11	88.11	184.04	143.05
50	0	98.59	106.59	184.50	151.91
51	0	132.03	140.03	190.38	146.77
52	0	168.53	176.53	177.25	144.03
53	0	97.97	105.97	223.22	151.08
54	0	251.16	259.16	210.44	136.79
55	0	80.46	88.46	186.65	145.98
56	0	93.55	101.55	187.21	148.08

57	0	139.50	147.50	269.13	142.93
58	0	125.82	133.82	188.05	143.91
59	0	143.54	151.54	203.44	153.84
60	0	194.86	202.86	258.57	147.72
61	0	187.86	195.86	254.92	147.72
62	0	384.95	392.95	223.87	147.91
63	0	141.26	149.26	196.36	147.89
64	0	176.76	184.76	198.68	149.83
65	0	96.18	104.18	207.99	152.04
66	0	127.02	135.02	238.65	140.63
67	0	120.91	128.91	248.60	140.31
68	0	170.29	178.29	204.54	149.20
69	0	74.05	82.05	166.12	141.10
70	0	124.58	132.58	189.64	144.21
71	0	128.91	136.91	184.24	145.84
72	0	187.09	195.09	258.33	145.10
73	0	96.12	104.12	194.07	144.33
74	0	117.17	125.17	197.99	147.58
75	0	168.99	176.99	178.61	139.13
76	0	120.56	128.56	197.30	146.85
77	0	102.80	110.80	204.60	152.61
78	0	80.38	88.38	232.77	145.87
79	0	101.37	109.37	195.51	157.46
80	0	177.22	185.22	181.24	150.17
81	0	83.87	91.87	195.10	149.13
82	0	86.97	94.97	219.18	146.08
83	0	153.35	161.35	242.64	148.83
84	0	125.68	133.68	186.07	151.49
85	0	209.92	217.92	207.43	145.54
86	0	424.59	432.59	226.42	145.06
87	0	81.50	89.50	200.59	148.01
88	0	100.57	108.57	249.62	153.94
89	0	130.54	138.54	183.88	146.02
90	0	159.28	167.28	187.37	151.06
91	0	174.59	182.59	189.54	149.45
92	0	132.52	140.52	278.55	150.79
93	0	279.13	287.13	257.53	157.11
94	0	148.05	156.05	272.61	152.59
95	0	117.79	125.79	224.80	154.80
96	0	94.28	102.28	177.09	152.05
97	0	191.55	199.55	195.70	153.30
98	0	112.87	120.87	181.94	152.12
99	0	83.79	91.79	189.78	155.96
100	0	177.13	185.13	164.63	153.89

Table S3: ΔAIC between the final model (Global model) and the null models fitted to initial frequency on each phylogenetic tree. See Table 3 in the main text for the description of the null models.

Tree	Global model	No coefficients	λ only	ϕ only	Independent
1	0	76.93	64.76	116.07	59.34
2	0	80.00	81.12	132.01	67.63
3	0	75.96	103.19	124.23	64.28
4	0	70.57	88.66	122.71	63.67
5	0	70.71	66.29	127.42	64.84
6	0	68.53	70.23	134.53	50.94
7	0	68.98	33.87	120.01	54.52
8	0	69.12	110.01	135.25	60.88
9	0	70.99	246.67	142.99	57.04
10	0	70.30	47.74	114.36	67.18
11	0	71.90	75.60	114.33	62.35
12	0	70.52	216.99	122.34	62.79
13	0	72.55	58.34	144.59	57.55
14	0	72.45	90.75	115.75	62.70
15	0	72.17	106.78	126.76	59.06
16	0	71.64	78.40	114.31	62.54
17	0	69.05	43.15	113.11	62.65
18	0	76.02	71.41	127.68	57.58
19	0	74.06	63.92	148.53	66.79
20	0	77.84	82.51	128.08	63.02
21	0	71.07	72.87	124.07	57.61
22	0	71.44	48.60	119.00	59.58
23	0	67.07	71.61	118.82	65.70
24	0	64.57	98.98	119.07	56.25
25	0	67.79	48.54	118.26	63.97
26	0	71.37	149.78	112.84	57.59
27	0	72.50	58.71	118.93	61.69
28	0	77.89	136.44	155.38	63.94
29	0	68.95	54.10	125.04	63.56
30	0	75.46	65.13	140.86	66.69
31	0	71.17	76.07	126.85	63.31
32	0	71.09	40.66	106.56	60.59
33	0	74.53	63.26	115.48	64.37
34	0	73.31	51.09	116.94	65.60
35	0	75.05	73.10	111.64	67.47
36	0	75.10	88.10	121.50	67.38
37	0	70.76	164.70	109.17	62.89
38	0	70.27	62.94	116.24	63.17
39	0	72.82	50.55	147.86	61.27
40	0	67.78	77.45	148.26	56.73
41	0	70.97	51.77	111.86	62.87
42	0	72.38	79.76	121.09	58.46
43	0	66.00	212.83	132.27	63.32
44	0	69.51	43.51	135.47	65.23
45	0	78.09	61.22	128.71	54.30
46	0	75.72	74.17	125.37	64.39
47	0	81.34	92.78	127.11	61.97
48	0	73.87	44.38	109.77	62.29
49	0	72.27	71.21	117.41	52.18
50	0	74.02	74.78	125.40	64.99
51	0	70.88	93.47	118.14	57.92
52	0	68.52	85.37	132.24	56.29
53	0	68.84	47.47	142.45	61.35
54	0	80.56	78.09	136.62	53.04
55	0	77.39	92.76	117.25	56.78
56	0	77.22	72.23	126.85	53.03

57	0	72.18	72.05	134.66	51.05
58	0	69.27	49.41	124.26	52.26
59	0	73.59	85.59	112.31	65.69
60	0	75.12	63.58	132.46	67.71
61	0	75.66	84.87	121.19	63.56
62	0	80.37	123.19	112.35	66.17
63	0	73.50	61.98	118.67	59.42
64	0	74.89	224.65	138.81	57.87
65	0	66.63	76.54	123.45	58.57
66	0	74.76	64.14	122.44	58.51
67	0	82.60	46.32	130.67	56.69
68	0	72.51	167.03	127.46	62.75
69	0	75.68	116.96	112.48	58.89
70	0	70.94	53.52	118.15	54.22
71	0	70.92	78.84	127.05	62.02
72	0	70.40	122.53	128.45	61.97
73	0	69.83	63.19	153.27	56.93
74	0	73.62	107.26	134.30	61.88
75	0	73.97	62.36	127.80	60.74
76	0	70.03	85.32	125.13	62.59
77	0	69.25	78.99	118.80	65.39
78	0	71.49	82.79	126.13	56.86
79	0	72.11	188.76	108.53	65.74
80	0	71.98	65.73	115.83	61.75
81	0	68.02	93.81	118.29	60.55
82	0	74.38	69.60	148.70	59.72
83	0	73.81	89.98	118.22	67.57
84	0	68.56	67.18	127.89	64.54
85	0	63.86	73.46	145.32	58.66
86	0	67.72	56.39	137.92	59.47
87	0	71.24	69.98	131.03	55.68
88	0	80.00	89.98	124.07	66.07
89	0	74.46	75.88	132.71	58.71
90	0	73.27	77.99	123.74	62.42
91	0	71.34	48.14	122.19	70.03
92	0	65.66	53.89	146.70	64.13
93	0	73.83	125.74	117.90	64.68
94	0	77.88	111.48	142.50	69.68
95	0	73.03	61.19	155.47	66.34
96	0	72.26	104.60	119.95	66.42
97	0	73.69	75.09	125.72	66.99
98	0	72.18	116.93	115.29	61.87
99	0	75.43	69.61	125.42	60.21
100	0	74.64	38.87	112.90	67.66

Table S4: ΔAIC between the final model (Global model) and the null models fitted to final frequency on each phylogenetic tree. See Table 3 in the main text for the description of the null models.

Tree	Global model	No coefficients	λ only	ϕ only	Independent
1	0	95.37	51.78	167.47	131.00
2	0	97.84	48.08	182.52	135.79
3	0	92.01	112.65	182.03	128.90
4	0	83.92	64.17	179.31	128.36
5	0	84.01	91.06	179.63	128.48
6	0	85.96	86.06	187.25	123.68
7	0	85.15	76.40	177.39	125.62
8	0	84.21	89.56	183.00	128.15
9	0	84.96	102.34	183.53	130.42
10	0	86.70	120.14	166.30	127.23
11	0	84.69	145.40	167.42	119.19
12	0	89.59	126.51	192.49	126.36
13	0	90.60	64.21	182.90	125.23
14	0	88.64	46.06	186.64	126.97
15	0	85.83	88.97	179.66	126.18
16	0	88.90	250.67	163.87	128.73
17	0	79.62	113.92	172.96	123.16
18	0	89.07	97.47	174.99	128.29
19	0	87.67	41.65	226.64	135.71
20	0	90.98	56.01	186.44	133.94
21	0	84.90	139.64	181.38	125.56
22	0	87.06	59.12	181.20	128.17
23	0	80.84	54.01	182.03	132.25
24	0	78.93	41.72	183.14	129.26
25	0	81.63	62.87	184.64	128.32
26	0	84.70	94.58	182.75	126.78
27	0	85.02	302.68	177.49	122.27
28	0	89.39	48.10	151.60	131.62
29	0	82.99	53.95	176.68	126.83
30	0	86.63	101.79	211.49	128.03
31	0	85.51	73.13	172.03	126.48
32	0	89.87	46.22	176.13	127.03
33	0	87.49	106.18	173.15	123.70
34	0	85.38	119.29	156.86	126.25
35	0	90.06	42.20	158.05	130.46
36	0	86.01	61.64	186.81	127.76
37	0	85.17	133.45	179.31	127.52
38	0	86.48	127.79	157.39	127.31
39	0	85.27	63.15	216.23	120.75
40	0	84.47	54.85	219.54	124.33
41	0	84.30	60.14	172.86	122.51
42	0	88.71	63.12	177.15	124.37
43	0	82.81	114.59	188.30	127.31
44	0	81.14	47.91	217.40	129.46
45	0	90.68	54.89	153.18	131.90
46	0	90.02	121.41	170.61	135.08
47	0	89.40	87.49	188.25	127.34
48	0	87.88	49.77	174.27	126.15
49	0	87.51	85.81	163.96	128.10
50	0	88.62	92.43	182.31	131.43
51	0	86.07	72.16	182.03	131.23
52	0	81.90	95.94	177.78	126.19
53	0	83.16	105.97	222.66	129.68
54	0	93.41	126.61	221.39	129.42
55	0	92.26	48.92	174.29	126.14
56	0	93.75	89.05	174.64	126.75

57	0	92.29	85.81	195.72	127.96
58	0	88.28	85.95	177.66	122.44
59	0	90.34	268.23	180.33	128.79
60	0	92.19	63.36	171.42	130.38
61	0	90.89	228.33	180.40	128.62
62	0	89.27	226.57	159.66	126.63
63	0	92.40	45.48	179.69	128.43
64	0	95.14	130.83	186.31	130.86
65	0	85.99	58.64	198.88	129.28
66	0	91.11	77.39	195.15	125.72
67	0	92.17	39.37	197.87	126.43
68	0	87.15	153.99	179.64	124.97
69	0	88.88	66.80	151.68	125.64
70	0	88.12	115.95	185.44	125.14
71	0	85.82	57.31	166.03	128.88
72	0	80.11	76.43	196.86	129.81
73	0	86.64	45.83	195.97	128.98
74	0	88.28	46.68	197.70	125.58
75	0	86.78	55.91	165.65	124.96
76	0	86.65	131.93	164.89	124.10
77	0	84.92	94.61	180.17	128.77
78	0	86.23	121.87	171.42	128.46
79	0	87.55	86.12	160.53	132.61
80	0	85.56	55.32	175.16	128.01
81	0	86.14	43.49	187.40	130.94
82	0	89.73	75.68	231.02	126.53
83	0	85.73	130.89	184.25	127.25
84	0	85.02	47.43	187.49	133.36
85	0	83.86	69.79	208.67	133.10
86	0	87.07	86.94	198.70	128.33
87	0	87.87	61.97	170.08	125.99
88	0	92.27	107.77	182.20	128.49
89	0	90.16	120.77	202.49	123.79
90	0	84.76	43.87	178.90	128.11
91	0	84.41	52.35	178.21	127.90
92	0	84.48	47.68	223.76	126.99
93	0	89.18	287.34	178.35	127.98
94	0	88.20	66.50	213.17	128.96
95	0	88.91	44.97	234.12	131.88
96	0	86.83	76.37	165.94	128.27
97	0	88.53	77.72	185.01	130.05
98	0	87.70	114.44	164.92	127.08
99	0	91.18	165.95	182.55	127.44
100	0	91.08	73.74	146.54	129.58

Table S5: ΔAIC between the final model (Global model) and the null models fitted to frequency bandwidth on each phylogenetic tree. See Table 3 in the main text for the description of the null models.

Tree	Global model	No coefficients	λ only	ϕ only	Independent
1	0	15.94	164.17	141.49	68.81
2	0	15.91	164.05	148.97	70.59
3	0	18.11	219.50	153.76	65.44
4	0	16.61	240.04	150.09	65.37
5	0	16.00	159.10	160.63	65.54
6	0	15.33	258.96	154.09	62.77
7	0	17.25	202.81	161.53	59.89
8	0	17.27	330.49	155.18	66.74
9	0	17.81	541.74	190.17	64.03
10	0	15.88	202.22	168.42	62.73
11	0	14.67	364.73	170.68	62.80
12	0	16.62	304.66	158.74	57.21
13	0	12.80	128.29	149.50	64.09
14	0	15.77	197.70	151.11	65.66
15	0	19.78	236.42	143.83	65.17
16	0	16.98	439.43	173.66	57.61
17	0	14.69	188.74	146.68	61.14
18	0	20.67	186.60	174.62	62.63
19	0	13.84	150.65	147.67	69.88
20	0	17.46	139.53	163.41	68.60
21	0	14.55	206.36	182.38	63.24
22	0	17.17	285.50	167.84	65.41
23	0	15.32	161.02	163.79	63.35
24	0	16.19	231.40	178.17	59.12
25	0	13.74	147.09	159.46	65.42
26	0	16.72	240.39	157.10	59.62
27	0	18.13	173.09	145.93	65.86
28	0	18.25	260.15	159.05	60.20
29	0	14.81	164.05	164.28	65.53
30	0	16.40	210.75	168.46	67.49
31	0	13.59	161.70	146.49	69.76
32	0	15.94	150.94	165.93	60.33
33	0	14.98	205.85	155.97	63.84
34	0	12.58	150.01	173.72	67.85
35	0	14.28	243.86	158.37	65.69
36	0	15.72	165.08	163.84	65.21
37	0	13.81	211.09	145.45	64.69
38	0	15.04	110.78	164.50	58.66
39	0	15.98	165.91	166.11	65.54
40	0	17.22	224.53	169.56	64.10
41	0	17.41	160.84	153.31	61.45
42	0	18.75	167.42	180.97	61.86
43	0	16.43	281.92	146.10	67.41
44	0	16.41	132.17	182.17	61.61
45	0	17.66	184.26	180.79	63.75
46	0	18.74	177.34	159.85	66.02
47	0	20.23	226.16	148.34	65.91
48	0	16.40	113.19	157.88	64.00
49	0	18.42	154.32	168.22	63.20
50	0	14.15	137.91	167.65	68.23
51	0	15.34	178.76	158.55	62.60
52	0	17.20	213.19	160.69	63.02
53	0	15.78	264.45	164.15	64.50
54	0	15.79	209.08	152.73	63.57
55	0	18.15	185.37	164.71	63.86
56	0	15.93	222.03	152.88	61.44

57	0	17.73	345.00	166.98	56.68
58	0	15.86	176.95	174.50	61.65
59	0	16.55	300.78	140.09	64.93
60	0	15.15	168.22	145.81	69.53
61	0	17.01	186.20	147.54	73.00
62	0	16.84	553.72	146.56	66.38
63	0	15.38	130.27	152.93	67.35
64	0	13.52	327.54	149.96	65.05
65	0	14.78	130.45	146.16	63.52
66	0	16.69	144.77	163.14	65.34
67	0	20.69	120.70	161.06	69.47
68	0	15.33	225.18	163.87	67.80
69	0	15.91	227.90	146.06	65.76
70	0	17.92	125.78	191.89	65.03
71	0	16.17	178.05	186.88	61.99
72	0	15.68	316.37	188.61	65.05
73	0	14.62	128.61	206.81	62.43
74	0	13.25	215.18	148.08	63.82
75	0	14.39	145.91	151.15	68.30
76	0	13.85	175.32	153.34	65.50
77	0	14.29	155.55	169.08	67.92
78	0	17.37	299.86	174.56	63.29
79	0	14.76	366.69	157.44	66.92
80	0	15.17	201.20	167.17	66.68
81	0	13.92	158.63	149.04	64.85
82	0	16.24	165.85	172.01	63.12
83	0	16.89	163.46	157.88	68.38
84	0	14.36	163.40	150.53	67.23
85	0	14.48	188.24	157.53	64.15
86	0	11.60	158.98	149.72	69.69
87	0	14.55	260.62	157.03	68.24
88	0	16.21	116.78	152.63	73.16
89	0	13.74	158.51	140.65	68.21
90	0	14.54	221.58	147.24	69.20
91	0	13.10	148.50	147.66	69.67
92	0	12.70	129.61	140.90	66.64
93	0	15.00	261.64	152.37	65.04
94	0	16.24	242.99	167.81	64.16
95	0	14.53	160.73	160.80	65.35
96	0	13.46	147.16	146.07	67.61
97	0	13.53	229.69	137.54	69.88
98	0	17.41	162.01	149.01	62.70
99	0	17.19	207.65	144.75	68.14
100	0	16.96	206.11	147.39	62.14

Table S6: ΔAIC between the final model (Global model) and the null models fitted to call duration on each phylogenetic tree. See Table 3 in the main text for the description of the null models.

Tree	Global model	No coefficients	λ only	ϕ only	Independent
1	0	60.25	38.27	169.03	292.23
2	0	55.63	65.51	169.97	284.02
3	0	57.67	27.92	149.45	288.38
4	0	55.35	36.72	165.96	286.98
5	0	52.29	42.13	160.53	281.53
6	0	51.71	71.04	167.08	276.13
7	0	56.32	49.92	186.21	280.57
8	0	55.44	95.36	167.77	278.82
9	0	56.35	66.86	164.07	281.56
10	0	56.28	65.31	176.36	283.02
11	0	56.60	128.53	169.90	282.87
12	0	53.19	233.13	147.79	279.60
13	0	53.33	64.18	169.39	282.62
14	0	53.46	69.20	150.51	280.08
15	0	58.54	115.57	160.66	284.69
16	0	57.25	67.41	180.56	288.83
17	0	55.64	64.90	149.01	282.55
18	0	59.74	59.97	182.50	286.20
19	0	56.68	48.35	157.29	286.64
20	0	56.03	40.63	178.54	279.27
21	0	58.94	111.56	165.00	283.31
22	0	56.57	65.17	151.63	283.83
23	0	58.83	92.63	168.52	284.30
24	0	56.07	60.63	162.44	281.42
25	0	56.84	42.15	192.47	284.67
26	0	54.58	127.81	140.95	276.76
27	0	57.24	132.92	150.55	282.78
28	0	59.80	60.15	167.69	286.23
29	0	58.23	53.62	176.73	282.31
30	0	62.48	80.07	175.03	287.14
31	0	62.26	35.75	156.50	292.44
32	0	58.26	26.21	176.64	287.05
33	0	58.52	43.82	175.07	290.41
34	0	58.69	126.29	153.29	285.49
35	0	53.20	83.19	179.43	282.06
36	0	53.84	148.80	192.29	285.73
37	0	53.04	112.54	146.37	283.52
38	0	57.48	30.52	182.36	289.34
39	0	57.09	46.21	180.85	284.57
40	0	56.01	43.49	151.49	280.91
41	0	50.96	72.48	170.26	282.81
42	0	56.93	40.17	162.10	287.00
43	0	58.05	255.47	175.40	287.05
44	0	58.23	69.15	167.79	280.79
45	0	62.50	58.97	174.95	283.62
46	0	61.65	122.98	165.15	283.19
47	0	58.51	59.03	143.28	282.05
48	0	54.63	58.50	170.37	283.21
49	0	56.60	77.58	167.60	283.54
50	0	57.25	39.51	168.25	282.80
51	0	57.14	58.40	149.92	283.51
52	0	57.53	50.97	175.02	281.69
53	0	57.28	82.68	147.44	279.86
54	0	60.11	23.98	179.20	279.82
55	0	57.42	34.23	169.26	280.78
56	0	56.11	42.63	157.17	284.16

57	0	54.50	294.83	155.43	277.70
58	0	52.88	38.79	181.57	281.72
59	0	58.34	153.76	148.13	280.58
60	0	57.79	74.67	165.03	278.95
61	0	59.85	139.62	164.11	285.96
62	0	59.38	77.09	152.57	284.35
63	0	55.36	76.22	169.01	279.84
64	0	57.69	154.65	182.66	287.01
65	0	52.09	70.90	151.87	283.50
66	0	55.20	38.23	166.26	278.44
67	0	62.28	21.51	167.60	280.08
68	0	54.33	134.69	181.11	284.25
69	0	54.80	71.95	195.01	285.90
70	0	62.09	124.43	158.39	281.49
71	0	53.10	45.73	173.34	283.89
72	0	51.27	99.94	155.31	286.26
73	0	54.72	37.25	160.82	283.02
74	0	58.50	71.06	176.48	283.26
75	0	54.59	82.69	174.39	281.56
76	0	51.04	64.71	171.53	284.44
77	0	53.76	60.43	160.52	284.80
78	0	57.79	70.56	177.81	288.70
79	0	54.61	121.09	174.18	286.89
80	0	55.93	90.57	151.60	285.73
81	0	57.24	38.45	151.18	284.40
82	0	56.69	28.60	156.74	283.74
83	0	56.05	92.72	172.65	282.63
84	0	55.74	61.92	163.61	288.01
85	0	53.88	34.44	161.86	281.66
86	0	57.64	52.58	174.17	284.19
87	0	58.46	66.80	165.48	279.65
88	0	57.77	33.34	151.97	280.46
89	0	54.87	61.19	176.65	279.88
90	0	58.53	57.30	168.54	283.07
91	0	57.25	40.48	152.74	281.13
92	0	52.97	55.30	170.16	281.55
93	0	55.73	63.50	157.32	281.71
94	0	60.37	68.13	174.03	281.44
95	0	55.25	45.58	193.32	279.68
96	0	62.79	38.09	196.51	283.57
97	0	59.13	70.11	154.24	288.02
98	0	57.02	82.89	164.96	283.56
99	0	56.48	94.87	178.67	279.42
100	0	54.20	97.29	171.98	279.12

Supplementary references:

1. Armstrong, K.N. & Coles, R.B. 2007. Echolocation call frequency differences between geographic isolates of Rhinonicteris aurantia (Chiroptera: Hipposideridae): implications of nasal chamber size. *J. Mammal.* **88**: 94–104.
2. Avila-Flores, R. & Fenton, M.B. 2005. Use of spatial features by foraging insectivorous bats in a large urban landscape. *J. Mammal.* **86**: 1193–1204.
3. Bambini, L., Kofoky, A.F., Mbohoahy, T., Ralisata, M., Manjoazy, T., Hosken, D.J., *et al.* 2011. Do bats need trees? Habitat use of two Malagasy hipposiderid bats Triaenops furculus and T. menamena in the dry southwest. *Hystrix - Ital. J. Mammal.* **22**: 81–92.
4. Barclay, R.M.R. 1986. The echolocation calls of hoary (Lasiurus cinereus) and silver-haired (Lasionycteris noctivagans) bats as adaptations for long- versus short-range foraging strategies and the consequences for prey selection. *Can. J. Zool.* **64**: 2700–2705.
5. Barclay, R.M.R., Fenton, M.B., Tuttle, M.D. & Ryan, M.J. 1981. Echolocation calls produced by Trachops cirrhosus (Chiroptera: Phyllostomatidae) while hunting for frogs. *Can. J. Zool.* **59**: 750–753.
6. Bell, G.P. 1985. The sensory basis of prey location by the California leaf-nosed bat Macrotus californicus (Chiroptera: Phyllostomidae). *Behav. Ecol. Sociobiol.* **16**: 343–347.
7. Benda, P., Dietz, C., Andreas, M., Hotovy, J., Lucan, R.K., Maltby, A., *et al.* 2008. Bats(Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 6. Bats of Sinai(Egypt) with some taxonomic, ecological and echolocation data on that fauna. *Acta Soc. Zool. Bohemicae* **72**: 1–103.
8. Benda, P., Radek, K.L., Obuch, J., Reiter, A., Andreas, M., Bačkor, P., *et al.* 2010. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 8. Bats of Jordan: fauna, ecology, echolocation, ectoparasites. *Acta Soc. Zool. Bohem* **74**: 185–353.
9. Biscardi, S., Orprecio, J., Fenton, M.B., Tsoar, A. & Ratcliffe, J.M. 2004. Data, sample sizes and statistics affect the recognition of species of bats by their echolocation calls. *Acta chiropterologica* **6**: 347–363.
10. Blood, B.R. & Clark, M.K. 1998. Myotis vivesi. *Mamm. species* 1–5.
11. Braun, J.K., Layman, Q.D. & Mares, M.A. 2009. Myotis albescens (Chiroptera: Vespertilionidae). *Mamm. Species* 1–9.
12. Brinklov, S., Jakobsen, L., Ratcliffe, J.M., Kalko, E.K. V & Surlykke, A. 2011. Echolocation call intensity and directionality in flying short-tailed fruit bats, Carollia perspicillata (Phyllostomidae). *J. Acoust. Soc. Am.* **129**: 427–435.
13. Brinkløv, S., Kalko, E. & Surlykke, A. 2010. Dynamic adjustment of biosonar intensity to habitat clutter in the bat Macrophyllum macrophyllum (Phyllostomidae). *Behav. Ecol. Sociobiol.* **64**: 1867–1874.
14. Brinkløv, S., Kalko, E.K. V & Surlykke, A. 2009. Intense echolocation calls from two `whispering' bats, Artibeus jamaicensis and Macrophyllum macrophyllum (Phyllostomidae). *J. Exp. Biol.* **212**: 11–20.
15. Briones-Salas, M., Peralta-Pérez, M. & García-Luis, M. 2013. Acoustic characterization of new species of bats for the State of Oaxaca, Mexico. *THERYA* **4**: 15–32.
16. Carter, G.G., Fenton, M.B. & Faure, P.A. 2009. White-winged vampire bats (Diaemus youngi) exchange contact calls. *Can. J. Zool.* **87**: 604–608.
17. Corcoran, A.J. 2007. Automated acoustic identification of nine bat species of the eastern United States. Humboldt State University.

18. Csada, R. 1996. Cardioderma cor. *Mamm. Species* 1–4.

19. Decher, J. & Fahr, J. 2005. Hipposideros cyclops. *Mamm. Species* 1–7.

20. Dietz, C. 2005. *Illustrated identification key to the bats of Egypt*. Version 1.0. Tuerbingen (Germany).

21. Douangboubpha, B., Bumrungsri, S., Soisook, P., Murray, S.W., Puechmaille, S.J., Satasook, C., *et al.* 2010. A Taxonomic Review of Hipposideros halophyllus, with Additional Information on H. ater and H. cineraceus (Chiroptera: Hipposideridae) from Thailand and Myanmar. *Acta Chiropterologica* **12**: 29–50.

22. Douangboubpha, B., Bumrungsri, S., Soisook, P., Satasook, C., Thomas, N.M. & Bates, P.J.J. 2010. A Taxonomic Review of the Hipposideros bicolor Species Complex and H. pomona (Chiroptera: Hipposideridae) in Thailand. *Acta Chiropterologica* **12**: 415–438.

23. Dzal, Y., Hooton, L.A., Clare, E.L. & Fenton, M.B. 2009. Bat Activity and Genetic Diversity at Long Point, Ontario, an Important Bird Stopover Site. *Acta Chiropterologica* **11**: 307–315.

24. Eger, J.L. & Fenton, M.B. 2003. Rhinolophus paradoxolophus. *Mamm. species* 1–4.

25. Estók, P. & Siemers, B.M. 2009. Calls of a Bird-Eater: The Echolocation Behaviour of the Enigmatic Greater Noctule, Nyctalus lasiopterus. *Acta Chiropterologica* **11**: 405–414.

26. Fahr, J. & Ebigbo, N.M. 2003. A conservation assessment of the bats of the Simandou Range, Guinea, with the first record of Myotis welwitschii (Gray, 1866) from West Africa. *Acta Chiropterologica* **5**: 125–141.

27. Fenton, M.B. & Bell, G.P. 1981. Recognition of species of insectivorous bats by their echolocation calls. *J. Mammal.* 233–243.

28. Fenton, M.B. & Fullard, J.H. 1979. The influence of moth hearing on bat echolocation strategies. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **132**: 77–86.

29. Fenton, M.B., Jacobs, D.S., Richardson, E.J., Taylor, P.J. & White, W. 2004. Individual signatures in the frequency-modulated sweep calls of African large-eared, free-tailed bats Otomops martiensseni (Chiroptera: Molossidae). *J. Zool.* **262**: 11–19.

30. Fenton, M.B., Portfors, C. V, Rautenbach, I.L. & Waterman, J.M. 1998. Compromises: Sound frequencies used in echolocation by aerial-feeding bats. *Can. J. Zool.* **76**: 1174–1182.

31. Fenton, M.B., Rautenbach, I.L., Rydell, J., Arita, H.T., Ortega, J., Bouchard, S., *et al.* 1998. Emergence, Echolocation, Diet and Foraging Behavior of Molossus ater (Chiroptera: Molossidae). *Biotropica* **30**: 314–320.

32. Fenton, M.B., Rydell, J., Vonhof, M.J., Eklöf, J. & Lancaster, W.C. 1999. Constant-frequency and frequency-modulated components in the echolocation calls of three species of small bats (Emballonuridae, Thyropteridae, and Vespertilionidae). *Can. J. Zool.* **77**: 1891–1900.

33. Fenton, M.B., Skowronski, M.D., McGuire, L.P. & Faure, P.A. 2011. Variation in the use of Harmonics in the Calls of Laryngeally Echolocating Bats. *Acta Chiropterologica* **13**: 169–178.

34. Fenton, M.B., Whitaker Jr, J.O., Vonhof, M.J., Waterman, J.M., Pedro, W.A., Aguiar, L., *et al.* 1999. The diet of bats from Southeastern Brazil: the relation to echolocation and foraging behaviour. *Rev. Bras. Zool.* **16**: 1081–1085.

35. Fukui, D., Agetsuma, N. & Hill, D.A. 2004. Acoustic Identification of Eight Species of Bat (Mammalia: Chiroptera) Inhabiting Forests of Southern Hokkaido, Japan: Potential for Conservation Monitoring. *Zoolog. Sci.* **21**: 947–955.

36. Fullard, J.H., Jackson, M.E., Jacobs, D.S., Pavey, C.R. & Burwell, C.J. 2008. Surviving cave bats: auditory and behavioural defences in the Australian noctuid moth, Speiredonia spectans. *J. Exp. Biol.* **211**: 3808–3815.

37. Fullard, J.H., Koehler, C., Surlykke, A. & McKenzie, N.L. 1991. Echolocation ecology and flight morphology of insectivorous bats (Chiroptera) in south-western Australia. *Aust. J. Zool.* **39**: 427–438.

38. Fullard, J.H., Ratcliffe, J.M. & Guignion, C. 2005. Sensory ecology of predator-prey interactions: responses of the AN2 interneuron in the field cricket, Teleogryllus oceanicus to the echolocation calls of sympatric bats. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **191**: 605–618.

39. Funakoshi, K. 2010. Acoustic identification of thirteen insectivorous bat species from the Kyushu District, Japan. *Mamm.* **50**: 165–175.

40. Gannon, W.L., Sherwin, R.E., de Carvalho, T.N. & O'Farrell, M.J. 2001. Pinnae and echolocation call differences between Myotis californicus and M. ciliolabrum (Chiroptera: Vespertilionidae). *Acta chiropterologica* **3**: 77–91.

41. Gillam, E.H., Chaverri, G., Montero, K. & Sagot, M. 2013. Social Calls Produced within and near the Roost in Two Species of Tent-Making Bats, Dermanura watsoni and Ectophylla alba. *PLoS One* **8**: e61731.

42. Goudy-Trainor, A. & Freeman, P.W. 2002. Call parameters and facial features in bats: a surprising failure of form following function. *Pap. Nat. Resour.* 18.

43. Guillén, A., Juste, B. & Ibáñez, C. 2000. Variation in the frequency of the echolocation calls of Hipposideros ruber in the Gulf of Guinea: an exploration of the adaptive meaning of the constant frequency value in rhinolophoid CF bats. *J. Evol. Biol.* **13**: 70–80.

44. Guillén-Servent, A. & Ibáñez, C. 2007. Unusual echolocation behavior in a small molossid bat, Molossops temminckii, that forages near background clutter. *Behav. Ecol. Sociobiol.* **61**: 1599–1613.

45. Hickey, M.B.C. & Dunlop, J.M. 2000. Nycteris grandis. *Mamm. Species* 1–4.

46. Hill, J.E. & Smith, S.E. 1981. Craseonycteris thonglongyai. *Mamm. species* 1–4.

47. Hood, C.S. & Pitocchelli, J. 1983. Noctilio albiventris. *Mamm. Species* 1–5.

48. Hughes, A.C., Satasook, C., Bates, P.J.J., Soisook, P., Sritongchuay, T., Jones, G., *et al.* 2010. Echolocation Call Analysis and Presence-Only Modelling as Conservation Monitoring Tools for Rhinolophoid Bats in Thailand. *Acta chiropterologica* **12**: 311–327.

49. Ibáñez, C., Juste, J., López-Wilchis, R., Albuja V, L., Núñez-Garduño, A. & O'Shea, T.J. 2002. Echolocation of three species of sac-winged bats (Balantiopteryx). *J. Mammal.* **83**: 1049–1057.

50. Ibáñez, C., Lopez-Wilchis, R., Javier, J.B. & León-Galván, M.A. 2000. Echolocation Calls and a Noteworthy Record of Pteronotus gymnonotus (Chiroptera, Mormoopidae) from Tabasco, Mexico. *Southwest. Nat.* **45**: 345–347.

51. Ith, S., Soisook, P., Bumrungsri, S., Kingston, T., Puechmaille, S.J., Struebig, M.J., *et al.* 2011. A Taxonomic Review of Rhinolophus coelophyllus Peters 1867 and R. shameli Tate 1943 (Chiroptera: Rhinolophidae) in Continental Southeast Asia. *Acta Chiropterologica* **13**: 41–59.

52. Jacobs, D., Barclay, R. & Walker, M. 2007. The allometry of echolocation call frequencies of insectivorous bats: why do some species deviate from the pattern? *Oecologia* **152**: 583–594.

53. Jacobs, D.S. & Barclay, R.M.R. 2009. Niche Differentiation in Two Sympatric Sibling Bat Species, Scotophilus Dinganii and Scotophilus Mhlanganii. *J. Mammal.* **90**: 879–887.

54. Jacobs, D.S., Barclay, R.M.R. & Schoeman, M.C. 2005. Foraging and roosting ecology of a rare insectivorous bat species, Laephotis wintoni (Thomas, 1901), Vespertilionidae. *Acta Chiropterologica* **7**: 101–109.

55. Jennings, N. V, Parsons, S., Barlow, K.E. & Gannon, M.R. 2004. Echolocation calls and wing morphology of bats from the West Indies. *Acta chiropterologica* **6**: 75–90.

56. Jones, G., Morton, M., Hughes, P.M. & Budden, R.M. 1993. Echolocation, flight morphology and foraging strategies of some West African hipposiderid bats. *J. Zool.* **230**: 385–400.

57. Jones, G., Webb, P.I., Sedgeley, J.A. & O'Donnell, C.F.J. 2003. Mysterious Mystacina: how the New Zealand short-tailed bat (Mystacina tuberculata) locates insect prey. *J. Exp. Biol.* **206**: 4209–4216.

58. Jung, K. & Kalko, E.K. V. 2011. Adaptability and vulnerability of high flying Neotropical aerial insectivorous bats to urbanization. *Divers. Distrib.* **17**: 262–274.

59. Jung, K., Kalko, E.K. V & Von Helversen, O. 2007. Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *J. Zool.* **272**: 125–137.

60. Jung, K., Molinari, J. & Kalko, E.K. V. 2014. Driving Factors for the Evolution of Species-Specific Echolocation Call Design in New World Free-Tailed Bats (Molossidae). *PLoS One* **9**: e85279.

61. Kalko, E.K. V & Condon, M.A. 1998. Echolocation, olfaction and fruit display: how bats find fruit of flagellichorous cucurbits. *Funct. Ecol.* **12**: 364–372.

62. Kalko, E.K. V, Schnitzler, H.U., Kaipf, I. & Grinnell, A.D. 1998. Echolocation and foraging behavior of the lesser bulldog bat, Noctilio albiventris: preadaptations for piscivory? *Behav. Ecol. Sociobiol.* **42**: 305–319.

63. Kingston, T., Jones, G., Akbar, Z. & Kunz, T.H. 1999. Echolocation signal design in Kerivoulinae and Murininae (Chiroptera: Vespertilionidae) from Malaysia. *J. Zool.* **249**: 359–374.

64. Kingston, T., Jones, G., Akbar, Z., Kunz, T.H. & O'Shea, T.J. 2003. Alternation of echolocation calls in 5 species of aerial-feeding insectivorous bats from Malaysia. *J. Mammal.* **84**: 205–215.

65. Kingston, T., Jones, G., Zubaid, A. & Kunz, T.H. 2000. Resource partitioning in rhinolophoid bats revisited. *Oecologia* **124**: 332–342.

66. Kofoky, A.F., Randrianandrianina, F., Russ, J., Raharinantenaina, I., Cardiff, S.G., Jenkins, R.K.B., *et al.* 2009. Forest Bats of Madagascar: Results of Acoustic Surveys. *Acta Chiropterologica* **11**: 375–392.

67. Korine, C. & Kalko, E. 2005. Fruit detection and discrimination by small fruit-eating bats (Phyllostomidae): echolocation call design and olfaction. *Behav. Ecol. Sociobiol.* **59**: 12–23.

68. Kunz, T.H. & Martin, R.A. 1982. Plecotus townsendii. *Mamm. species* 1–6.

69. Kwiecinski, G.G. 2006. Phyllostomus discolor. *Mamm. Species* 1–11.

70. Li, G., Liang, B., Wang, Y., Zhao, H., Helgen, K.M., Lin, L., *et al.* 2007. Echolocation Calls, Diet, and Phylogenetic Relationships of Stoliczka's Trident Bat, Aselliscus stoliczkanus (Hipposideridae). *J. Mammal.* **88**: 736–744.

71. Luo, F., Ma, J., Li, A., Wu, F.J., Chen, Q.C. & Zhang, S.Y. 2007. Echolocation Calls and Neurophysiological Correlations with Auditory Response Properties in the Inferior Colliculus of Pipistrellus abramus(Microchiroptera: Vespertilionidae). *Zool. Stud.* **46**: 622–630.

72. Ma, J., Liang, B., Zhang, S. & Metzner, W. 2008. Dietary composition and echolocation call design of three sympatric insectivorous bat species from China. *Ecol. Res.* **23**: 113–119.

73. MacDonald, K., Matsui, E., Stevens, R. & Fenton, M.B. 1994. Echolocation calls and field identification of the eastern pipistrelle (Pipistrellus subflavus: Chiroptera: Vespertilionidae), using ultrasonic bat detectors. *J. Mammal.* **75**: 462–465.

74. Macías, S., Mora, E.C. & García, A. 2006. Acoustic identification of mormoopid bats: a survey during the evening exodus. *J. Mammal.* **87**: 324–330.

75. Macias, S., Mora, E.C., Garcia, A. & Macias, Y. 2006. Echolocation Behavior of Brachyphylla nana (Chiroptera: Phyllostomidae) under Laboratory Conditions. *Caribb. J. Sci.* **42**: 114.

76. Macías, S., Mora, E.C., Koch, C. & Von Helversen, O. 2005. Echolocation behaviour of Phyllops falcatus (Chiroptera: Phyllostomidae): unusual frequency range of the first harmonic. *Acta Chiropterologica* **7**: 275–283.

77. MacSwiney, G.M., Bolívar, B., Clarke, F.M. & Racey, Y.P.A. 2006. Nuevos registros de Pteronotus personatus y Cynomops mexicanus (Chiroptera) en el estado de Yucatán, México. *Rev. Mex. Mastozoología* **10**: 102–109.

78. MacSwiney G., M.C., Bolívar Cimé, B., Clarke, F.M. & Racey, P.A. 2009. Insectivorous Bat Activity at Cenotes in the Yucatan Peninsula, Mexico. *Acta Chiropterologica* **11**: 139–147.

79. MacSwiney G., M.C., Clarke, F.M. & Racey, P.A. 2008. What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. *J. Appl. Ecol.* **45**: 1364–1371.

80. Medina, H., Lacher, T. & Woolley, J. 2011. Characteristics of echolocation calls of bats in Dominica.

81. Miller-Butterworth, C.M., Eick, G., Jacobs, D.S., Schoeman, M.C. & Harley, E.H. 2005. Genetic and phenotypic differences between South African long-fingered bats, with a global Miniopterinae phylogeny. *J. Mammal.* **86**: 1121–1135.

82. Milne, D.J. 2006. Habitat relationships, activity patterns and feeding ecology of insectivorous bats of the top end of Australia. James Cook University.

83. Milne, D.J., Reardon, T.B. & Watt, F. 2003. New records for the Arnhem sheathtail bat Taphozous kapalgensis (Chiroptera: Emballonuridae) from voucher specimens and Anabat recordings. *Aust. Zool.* **32**: 439–445.

84. Monadjem, A., Reside, A. & Lumsden, L. 2007. Echolocation calls of rhinolophid and hipposiderid bats in Swaziland. *South African J. Wildl. Res.* **37**: 9–15.

85. Monadjem, A., Schoeman, M.C., Reside, A., Pio, D. V, Stoffberg, S., Bayliss, J., *et al.* 2010. A Recent Inventory of the Bats of Mozambique with Documentation of Seven New Species for the Country. *Acta Chiropterologica* **12**: 371–391.

86. Monadjem, A., Taylor, P.J., Cotterill, W. & Schoeman, M.C. 2010. *Bats of southern and central Africa: a biogeographic and taxonomic synthesis*. Wits University Press Johannesburg.

87. Mora, E. & Macías, S. 2007. Echolocation calls of Poey's flower bat (Phyllonycteris poeyi) unlike those of other phyllostomids. *Naturwissenschaften* **94**: 380–383.

88. Mora, E.C., Ibáñez, C., Macías, S., Juste, J., López, I. & Torres, L. 2011. Plasticity in the Echolocation Inventory of Mormopterus minutus (Chiroptera, Molossidae). *Acta Chiropterologica* **13**: 179–187.

89. Mora, E.C. & Torres, L. 2008. Echolocation in the Large Molossid Bats Eumops glaucinus and Nyctinomops macrotis. *Zoolog. Sci.* **25**: 6–13.

90. Murray, K.L., Britzke, E.R. & Robbins, L.W. 2001. Variation in search-phase calls of bats. *J. Mammal.* **82**: 728–737.

91. Murray, K.L., Fraser, E., Davy, C., Fleming, T.H. & Fenton, M.B. 2009. Characterization of the Echolocation Calls of Bats from Exuma, Bahamas. *Acta Chiropterologica* **11**: 415–424.

92. Neuweiler, G., Metzner, W., Heilmann, U., Rübsamen, R., Eckrich, M. & Costa, H.H. 1987. Foraging behaviour and echolocation in the rufous horseshoe bat (Rhinolophus rouxi) of Sri Lanka. *Behav. Ecol. Sociobiol.* **20**: 53–67.

93. O'Farrell, M.J. & Miller, B.W. 1997. A new examination of echolocation calls of some neotropical bats (Emballonuridae and Mormoopidae). *J. Mammal.* 954–963.

94. O'Farrell, M.J., Miller, B.W. & Gannon, W.L. 1999. Qualitative identification of free-flying bats using the Anabat detector. *J. Mammal.* **80**: 11–23.

95. Obrist, M.K., Boesch, R. & Flückiger, P.F. 2004. Variability in echolocation call design of 26 Swiss bat species: consequences, limits and options for automated field identification with a synergetic pattern recognition approach. *Mammalia* **68**: 307–322.

96. Obrist, M.K., Fenton, M.B., Eger, J.L. & Schlegel, P.A. 1993. What ears do for bats: a comparative study of pinna sound pressure transformation in chiroptera. *J Exp Biol* **180**: 119–152.

97. Orozco-Lugo, L., Guillén-Servent, A., Valenzuela-Galván, D. & Arita, H.T. 2013. Descripción de los pulsos de ecolocalización de once especies de murciélagos insectívoros aéreos de una selva baja caducifolia en Morelos, México. *Therya* **4**: 33–46.

98. Ossa, G. 2010. Analysis of the echolocation calis and morphometry of a population of Myotis chiloensis (Waterhouse, 1838) from the southern Chilean temperate forest. *Cienc. Inv. Agr* 131–139.

99. Papadatou, E., Butlin, R.K. & Altringham, J.D. 2008. Identification of bat species in Greece from their echolocation calls. *Acta Chiropterologica* **10**: 127–143.

100. Parsons, S. 2001. Identification of New Zealand bats (Chalinolobus tuberculatus and Mystacina tuberculata) in flight from analysis of echolocation calls by artificial neural networks. *J. Zool.* **253**: 447–456.

101. Parsons, S. 1997. Search-phase echolocation calls of the New Zealand lesser short-tailed bat (Mystacina tuberculata) and long-tailed bat (Chalinolobus tuberculatus). *Can. J. Zool.* **75**: 1487–1494.

102. Parsons, S. & Jones, G. 2000. Acoustic identification of twelve species of echolocating bat by discriminant function analysis and artificial neural networks. *J. Exp. Biol.* **203**: 2641–2656.

103. Pavey, C., Grunwald, J.-E. & Neuweiler, G. 2001. Foraging habitat and echolocation behaviour of Schneider's leafnosed bat, Hipposideros speoris, in a vegetation mosaic in Sri Lanka. *Behav. Ecol. Sociobiol.* **50**: 209–218.

104. Pennay, M., Law, B., Reinhold, L., Wales, N.S., Wales, N.S. & Wales, N.S. 2004. *Bat calls of New South Wales: region based guide to the echolocation of microchiropteran bats*. Department of Environment and Conservation.

105. Phauk, S., Phen, S. & Furey, N.M. 2013. Cambodian bat echolocation: a first description of assemblage call param- eters and assessment of their utility for species identification. *Cambodian J. Nat. Hist.* 16–26.

106. Pio, D.V. V, Clarke, F.M., MacKie, I. & Racey, P.A. 2010. Echolocation Calls of the Bats of Trinidad, West Indies: Is Guild Membership Reflected in Echolocation Signal Design? *Acta chiropterologica* **12**: 217–229.

107. Portfors, C. V, Fenton, M.B., Aguiar, L.M.S., Baumgarten, J.E., Vonhof, M.J., Bouchard, S., *et al.* 2000. Bats from Fazenda Intervales, Southeastern Brazil: species account and comparison between different sampling methods. *Rev. Bras. Zool.* **17**: 533.

108. Pottie, S.A., Lane, D.J.W., Kingston, T. & Y.-H. Lee, B.P. 2005. The microchiropteran bat fauna of Singapore. *Acta Chiropterologica* **7**: 237–247.

109. Rainho, A., Marques, J. & Palmeirim, J.M. 2002. Os morcegos dos arquipélagos dos Açores e da Madeira: um contributo para a sua conservação. Instituto da Conservação da Natureza, Lisboa.

110. Ramasindrazana, B., Goodman, S.M., Schoeman, M.C. & Appleton, B. 2011. Identification of cryptic species of Miniopterus bats (Chiroptera: Miniopteridae) from Madagascar and the Comoros using bioacoustics overlaid on molecular genetic and morphological characters. *Biol. J. Linn. Soc.* **104**: 284–302.

111. Ratcliffe, J.M., Raghuram, H., Marimuthu, G., Fullard, J.H. & Fenton, M.B. 2005. Hunting in unfamiliar space: echolocation in the Indian false vampire bat, Megaderma lyra, when gleaning prey. *Behav. Ecol. Sociobiol.* **58**: 157–164.

112. Redgwell, R.D., Szewczak, J.M., Jones, G. & Parsons, S. 2009. Classification of echolocation calls from 14 species of bat by support vector machines and ensembles of neural networks. *Algorithms* **2**: 907–924.

113. Rodríguez-San Pedro, A. & Simonetti, J.A. 2013. Acoustic identification of four species of bats (Order Chiroptera) in central Chile. *Bioacoustics* **22**: 165–172.

114. Russo, D. & Jones, G. 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *J. Zool.* **258**: 91–103.

115. Rydell, J., Arita, H.T., Santos, M. & Granados, J. 2002. Acoustic identification of insectivorous bats (order Chiroptera) of Yucatan, Mexico. *J. Zool.* **257**: 27–36.

116. Salsamendi, E., Aihartza, J., Goiti, U., Almenar, D. & Garin, I. 2006. Echolocation calls and morphology in the Mehelyis (Rhinolophus mehelyi) and mediterranean (R. euryale) horseshoe bats: implications for resource partitioning. *Hystrix-the Ital. J. Mammal.* **16**.

117. Schaub, A. & Schnitzler, H.-U. 2007. Flight and echolocation behaviour of three vespertilionid bat species while commuting on flyways. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **193**: 1185–1194.

118. Schmieder, D.A., Kingston, T., Hashim, R. & Siemers, B.M. 2010. Breaking the trade-off: rainforest bats maximize bandwidth and repetition rate of echolocation calls as they approach prey. *Biol. Lett.* **6**: 604–609.

119. Schnitzler, H.U., Kalko, E.K. V, Kaipf, I. & Grinnell, A.D. 1994. Fishing and echolocation behavior of the greater bulldog bat, Noctilio leporinus, in the field. *Behav. Ecol. Sociobiol.* **35**: 327–345.

120. Schoeman, C. & Jacobs, D. 2003. Support for the allotonic frequency hypothesis in an insectivorous bat community. *Oecologia* **134**: 154–162.

121. Schoeman, M.C. & Jacobs, D.S. 2008. The Relative Influence of Competition and Prey Defenses on the Phenotypic Structure of Insectivorous Bat Ensembles in Southern Africa. *PLoS One* **3**: e3715.

122. Sedlock, J.L. & Weyandt, S.E. 2009. Genetic divergence between morphologically and acoustically cryptic bats: novel niche partitioning or recent contact? *J. Zool.* **279**: 388–395.

123. Siemers, B., Kalko, E. & Schnitzler, H.-U. 2001. Echolocation behavior and signal plasticity in the Neotropical bat Myotis nigricans (Schinz, 1821) (Vespertilionidae): a convergent case with European species of Pipistrellus? *Behav. Ecol. Sociobiol.* **50**: 317–328.

124. Smotherman, M. & Guillen-Servent, A. 2008. Doppler-shift compensation behavior by Wagner's mustached bat, Pteronotus personatus. *J. Acoust. Soc. Am.* **123**: 4331–4339.

125. Soisook, P., Niyomwan, P., Srikrachang, M., Srithongchuay, T. & Bates, P.J.J. 2010. Discovery of Rhinolophus beddomei (Chiroptera: Rhinolophidae) from Thailand with a Brief Comparison to Other Related Taxa. *Trop. Nat. Hist.* **10**.

126. Sripathi, K., Raghuram, H. & Nathan, P.T. 2006. Echolocation sounds of the painted bat Kerivoula picta (Vespertilionidae). *Curr. Sci.* **91**: 1145.

127. Struebig, M.J., Rossiter, S.J., Bates, P.J.J., Kingston, T., Lin Oo, S.S., Nwe, A.A., *et al.* 2005. Results of a recent bat survey in Upper Myanmar including new records from the Kachin forests. *Acta Chiropterologica* **7**: 147–163.

128. Sun, K., Feng, J., Jin, L., Liu, Y. & Jiang, Y. 2008. Identification of sympatric bat species by the echolocation calls. *Front. Biol. China* **3**: 227–231.

129. Surlykke, A., Jakobsen, L., Kalko, E.K. V & Page, R.A. 2013. Echolocation intensity and directionality of perching and flying fringe-lipped bats, Trachops cirrhosus (Phyllostomidae). *Front. Physiol.* **4**: PMC3695372.

130. Surlykke, A., Miller, L.A., Møhl, B., Andersen, B.B., Christensen-Dalsgaard, J. & Buhl Jørgensen, M. 1993. Echolocation in two very small bats from Thailand Craseonycteris thonglongyai and Myotis siligorensis. *Behav. Ecol. Sociobiol.* **33**: 1–12.

131. Taylor, P.J. 1999. Echolocation calls of twenty southern African bat species. *South African J. Zool.* **34**: 114–124.

132. Teixeira, S. & Jesus, J. 2009. Echolocation Calls of Bats from Madeira Island: Acoustic Characterization and Implications for Surveys. *Acta Chiropterologica* **11**: 183–190.

133. Thabah, A., Li, G., Wang, Y., Liang, B., Hu, K., Zhang, S., *et al.* 2007. Diet, Echolocation Calls, and Phylogenetic Affinities of the Great Evening Bat (Ia io; Vespertilionidae): Another Carnivorous Bat. *J. Mammal.* **88**: 728–735.

134. Thabah, A., Rossiter, S.J., Kingston, T., Zhang, S., Parsons, S., Mya, K.M.Y.A., *et al.* 2006. Genetic divergence and echolocation call frequency in cryptic species of Hipposideros larvatus s.l. (Chiroptera: Hipposideridae) from the Indo-Malayan region. *Biol. J. Linn. Soc.* **88**: 119–130.

135. Thies, W., Kalko, E.K. V & Schnitzler, H.-U. 1998. The roles of echolocation and olfaction in two Neotropical fruit-eating bats, Carollia perspicillata and C. castanea , feeding on Piper. *Behav. Ecol. Sociobiol.* **42**: 397–409.

136. Wei, L., Han, N., Zhang, L., Helgen, K.M., Parsons, S., Zhou, S., *et al.* 2008. Wing morphology, echolocation calls, diet and emergence time of black-bearded tomb bats (Taphozous melanopogon, Emballonuridae) from southwest China. *Acta Chiropterologica* **10**: 51–59.

137. Weinbeer, M. & Kalko, E. 2007. Ecological niche and phylogeny: the highly complex echolocation behavior of the trawling long-legged bat, Macrophyllum macrophyllum. *Behav. Ecol. Sociobiol.* **61**: 1337–1348.

138. Zhang, L., Jones, G., Zhang, J., Zhu, G., Parsons, S., Rossiter, S.J., *et al.* 2009. Recent Surveys of Bats (Mammalia: Chiroptera) from China. I. Rhinolophidae and Hipposideridae. *Acta Chiropterologica* **11**: 71–88.

139. Zhang, L., Liang, B., Parsons, S., Wei, L. & Zhang, S. 2007. Morphology, echolocation and foraging behaviour in two sympatric sibling species of bat (Tylonycteris pachypus and Tylonycteris robustula) (Chiroptera: Vespertilionidae). *J. Zool.* **271**: 344–351.

140. Zhang, L., Lu, L., Zhou, S., Dai, Q., Zhao, H., Guo-hua, L., *et al.* 2002. Comparison of the Echolocation Signals in Two Species of Flat-headed Bats at Flying. *Zool. Res.* **23**: 296–300.

141. Zhang, S., Zhao, H., Feng, J., Sheng, L., Li, Z. & Wang, L. 2000. Echolocation calls of Myotis frater (Chiroptera: Vespertilionidae) during search flight. *Chinese Sci. Bull.* **45**: 1690–1692.

CAPÍTULO 2

THE TEMPO OF ECHOLOCATION EVOLUTION

2.1 Introduction

Powered flight and echolocation are probably the main keys to the exceptional diversity of bats (Simmons 2005, Jones & Teeling 2006). Almost 85% of all known bat species are capable of echolocating through sounds produced in their larynx (Schuller & Moss 2004), an active process that enables them to navigate and forage in the dark (Griffin 1946, Griffin *et al.* 1960, Korine & Kalko 2005). Several studies dealt with the question of whether echolocation or flight appeared first (e.g. Fenton *et al.* 1995, Norberg 1994, Speakman 1993, reviewed in Denzinger *et al.* 2004), as well as whether echolocation evolved once or twice (Teeling *et al*. 2000, 2005, Eick *et al.* 2005, Teeling 2009). Recently this debate was reinforced by the discovery of a form of echolocation based on wing clicks in species from three distant subfamilies within Pteropodidae (Boonman *et al.* 2014), in which only one genus was known to echolocate by means of tong clicks (Yovel *et al.* 2010). This process, however, is different from the tonal calls produced in the other 18 bat families (Boonman *et al*. 2014, Fenton & Ratcliffe 2014). Despite the number of studies dealing with the origin of echolocation, the dynamics of its evolution within the laryngeal echolocating bats is still poorly understood.

Tonal bat echolocation (hereafter 'echolocation') is produced in a variety of call types or "shapes" that depict the relationship between call frequency and duration (Neuweiler 1989, Jones & Holderied 2007), with some remarkable cases of convergence of call types among distantly related groups (Jones & Teeling 2006, Maltby *et al.* 2012). The most conspicuous differentiation – between high (HDC) and low duty-cycle (LDC) echolocation (Fenton *et al.* 1995, 2012) – describes the relationship between call duration and interval, dividing the majority of species that use LDC and separate echoes in time (Kalko & Schnitzler 1989) from the HDC species, which emit long constant frequency calls separated by short intervals and are capable of discriminate echoes based on frequency alterations rather than time (Bell & Fenton 1984). HDC also represents the most prominent case of call type convergence, with the presence of HDC echolocation in two families from the Old World Rhinolophoidea and in one distantly related species from the New World,

Pteronotus parnellii. More generally, call types can be differentiated according to the amplitude of frequencies spanned within a call (Schnitzler *et al.* 2003), basically dividing bats in broadband, narrowband and constant frequency echolocators, which in turn are subdivided based on harmonic composition and call intensity (Jones & Teeling 2006).

Call types can be associated with the range and directionality of echolocation (Holderied *et al.* 2006, Jones & Holderied 2007), and bats can adjust multiple call and behavioral parameters to suitably probe the environment (Holderied & von Helversen 2003, Jakobsen *et al.* 2012, 2013). Consequently, differences in call structure are assumed to have a close relationship with the primary habitats occupied by the species (Schnitzler & Kalko 1998, 2001, Schnitzler *et al.* 2003, Surlykke & Kalko 2008). Narrowband signals are mainly associated with open habitats. Characterized by low frequency and high intensity (Jung *et al.* 2014), these calls can span for long distances and are best suited to the capture of insects in flight. The use of multiple harmonics within this type of call can be associated with hunting in open space close to vegetation or water streams (Jung *et al.* 2007). Broadband signals, on the other hand, are best suited for locating prey surrounded by clutter. In this type of call, a wide range of frequencies are covered within short time intervals (Schnitzler *et al.* 2003, Jones & Teeling 2006) guaranteeing a more precise time determination of echo return, facilitating the differentiation between prey items and the background (Moss & Surlykke 2010). The inclusion of higher harmonics within broadband signals provides information about the background that differs in frequency from those of the harmonic with most energy (Bates & Simmons 2010, Bates *et al.* 2011). Constant frequency HDC echolocation is probably the most specialized form of echolocation (Fenton *et al.* 2012). These species commonly occupy narrow space habitats and prey on moving insects (Jones & Teeling 2006), being capable of differentiate prey sizes based on the frequency alterations caused by the insect's wing-beating (Emde & Schnitzler 1990, Koselj *et al.* 2011).

In addition to the relation with habitat use and foraging mode, echolocation has an intrinsic relationship with body size (Aldridge & Rautenbach 1987, Norberg

& Rayner 1987). Call frequency is inversely scaled with forearm length (Jones 1999, Bilski *et al.* – Chapter 1), a property that confers a similar sonar beam shape ('field of view') to disparately sized species (Jakobsen *et al.* 2012). Call emission has an energetic cost as high as powered flight (Speakman *et al.* 1989), but through coupling its emission with wing beating, this elevated energy requirement is cancelled (Speakman & Racey 1991, Voigt & Lewanzik 2012). However, in LDC species, the emission rate must be adjusted to avoid the masking of successive calls and returning echoes (Schnitzler & Kalko 2001, Schintzler *et al.* 2003), a task that depends on the call frequency and intensity, and its attenuation through the atmosphere (Lawrence & Simmons 1982). To avoid this masking, larger species, which emit lower frequency calls, tend not to call at every wing beating (Holderied & von Helversen 2003). The frequency of maximum energy and the forearm length, thereby, may reflect the relationship between the extrinsic and intrinsic forces that shape the biosonar. However, determining how this allometric scaling and the habitat structuring of echolocation design affects the pace of phenotypic evolution and translates into different rates of frequency and size differentiation among clades, is an open question.

Describing the tempo of phenotypic evolution, the rate at which variance accumulates through time, is essential for understanding how it is produced and maintained (Adams 2013), and the adoption of an explicit phylogenetic context is paramount in the comparison of phenotypic variances among related groups (O'Meara *et al.* 2006, Adams *et al.* 2009). Rates of phenotypic evolution can vary among clades due to geographical isolation (Harmon *et al.* 2008, Wiens *et al.* 2011), as well as differences in morphological (Puttick *et al.* 2014), ecological (Thomas *et al.* 2009, Davis *et al.* 2014, Kaliontzopoulou *et al.* 2015) and behavioral characteristics (Thomas *et al.* 2006). The ecological release associated with the colonization of a different habitat or niche dimension (Mahler *et al.* 2010, Yoder *et al.* 2010) is commonly associated with the acceleration in rates of diversification (Losos & Miles 2002, Alfaro *et al.* 2009) and phenotypic differentiation. Despite that, Harmon *et al.* (2010) found little evidence for adaptive radiations (or 'early bursts') of morphological disparity in several animal taxa (not including Chiroptera),

implying that characters continue to differentiate after the species diversification reaches some equilibrium (Rabosky & Lovette 2008, Yoder *et al.* 2010). Hence, differences in ecological conditions and bursts of lineage diversification do not necessarily lead to different rates of phenotypic evolution.

In this paper, we aim to investigate if the different types of echolocation are associated with different rates of phenotypic evolution of frequency of maximum energy and forearm length. Moreover, we aim to examine if the convergence of echolocation types leads to convergent rates of evolution among groups that echolocate in the same manner. We investigate that through a series of hypotheses of phenotypic differentiation among and within clades. For ease of interpretation, we accounted for different rates only within a Brownian motion model of evolution (Felsenstein 1985, Pagel 1999, Freckleton *et al.* 2002), with multiple rates (O'Meara *et al.* 2006, Thomas *et al.* 2006). Although this model is often taken to represent just a process of neutral evolution (Butler & King 2004), other processes like directional selection towards a varying optima and punctuated evolution are also appropriately modeled by a Brownian motion model (Hansen & Martins 1996, O'Meara *et al.* 2006). Although the use of evolutionary models based on the Ornstein-Uhlenbeck process, which directly specify the presence and attraction to selective regimes (Hansen 1997), appears more compelling, Ho & Ané (2014) recently revealed problems associated with the maximum likelihood estimation of its parameters, and the preference for this model in data driven approaches may be more a statistical property of large datasets than a real biological attribute (Pennell *et al.* 2014a).

2.2 Material and Methods

We gathered data on echolocation calls of 372 bats species (39% of the echolocating bat species according to Wilson & Reeder 2005. See supplementary Table S1 for a description of the dataset representativeness) from published articles, field guides and theses (see supplementary Table S2 for the references

used). Only calls explicitly measured during the search phase (Griffin *et al.* 1960) were used. For species with more than one data source, we computed weighted averages considering the number of calls reported in each source, assuming it to be one single call when this information was absent. Forearm lengths of these species were collected at the Royal Ontario Museum mammalian collection, supplemented with data from the PanTHERIA database (Jones *et al.* 2009).

The most complete bat phylogeny to date is part of the mammalian supertree of Bininda-Emonds *et al.* (2007, 2008). Although Fritz *et al.* (2009) updated and corrected this supertree species nomenclature based on Wilson & Reeder (2005), we still found 61 cases of incorrect bat species names, and manually corrected them throughout the phylogeny. This tree, however, is only 51% resolved, so we used 100 time-calibrated trees randomly sampled from the Bayesian pseudo-posterior distribution of trees provided by Kuhn *et al.* (2011) to build a maximum clade credibility tree (hereafter mccTree) using the program TreeAnnotator 1.7.5 from the Beast software package (Drummond *et al.* 2012).

We evaluated 18 hypotheses of differential rates of evolution of frequency of maximum energy (FME) using the R package `OUwie` 1.4.4 (Beaulieu *et al.* 2012), under a Brownian motion model of evolution (see O'Meara *et al.* 2006 for a full description of this approach, and also Thomas *et al.* 2006). The null hypothesis of a single homogeneous rate across all clades was tested against alternative hypotheses based on the classification of echolocation types made by Jones & Teeling (2006), which categorize bats in eight categories based on the general structure of their echolocation calls. Although they recognize that these categories are not representative of all species in any given family, arguing that they can vary according to habitat and specific behaviors, we here consider these structures to be ubiquitous among species within most families, except Mormoopidae and Vespertilionidae. Variations within families are, at least to some extent, captured by the different evaluated hypotheses.

In the initial scenario, H1, all species within each family were classified in one of the following categories: constant frequency – CF; narrowband multiharmonic –

NM; short, broadband multiharmonic – SBM; narrowband fundamental harmonic – NF; short, broadband, fundamental harmonic - SBF; and polymorphic – P (see Jones & Teeling 2006 for the full call structure descriptions). The polymorphic classification adopted herein comprises those species that intermingle frequency modulated and constant frequency portions within a call, namely Noctilionidae and Mormoopidae – with the exception of *Pteronotus parnellii*, which was classified as CF. For Vespertilionidae, we classified most members as SBF, and those species in which the initial frequency is less than one octave higher than the final frequency (Schnitzler & Kalko 2001) were classified as NF. The other 16 hypothetical scenarios were composed of simplifications of this classification (Figure 1, Table 1), aggregating species and families according to the reconstructed ancestral states of the clades to which they pertain, and also a simpler classification differing bats into HDC and LDC callers (Fenton *et al.* 1995, Fenton 2012).

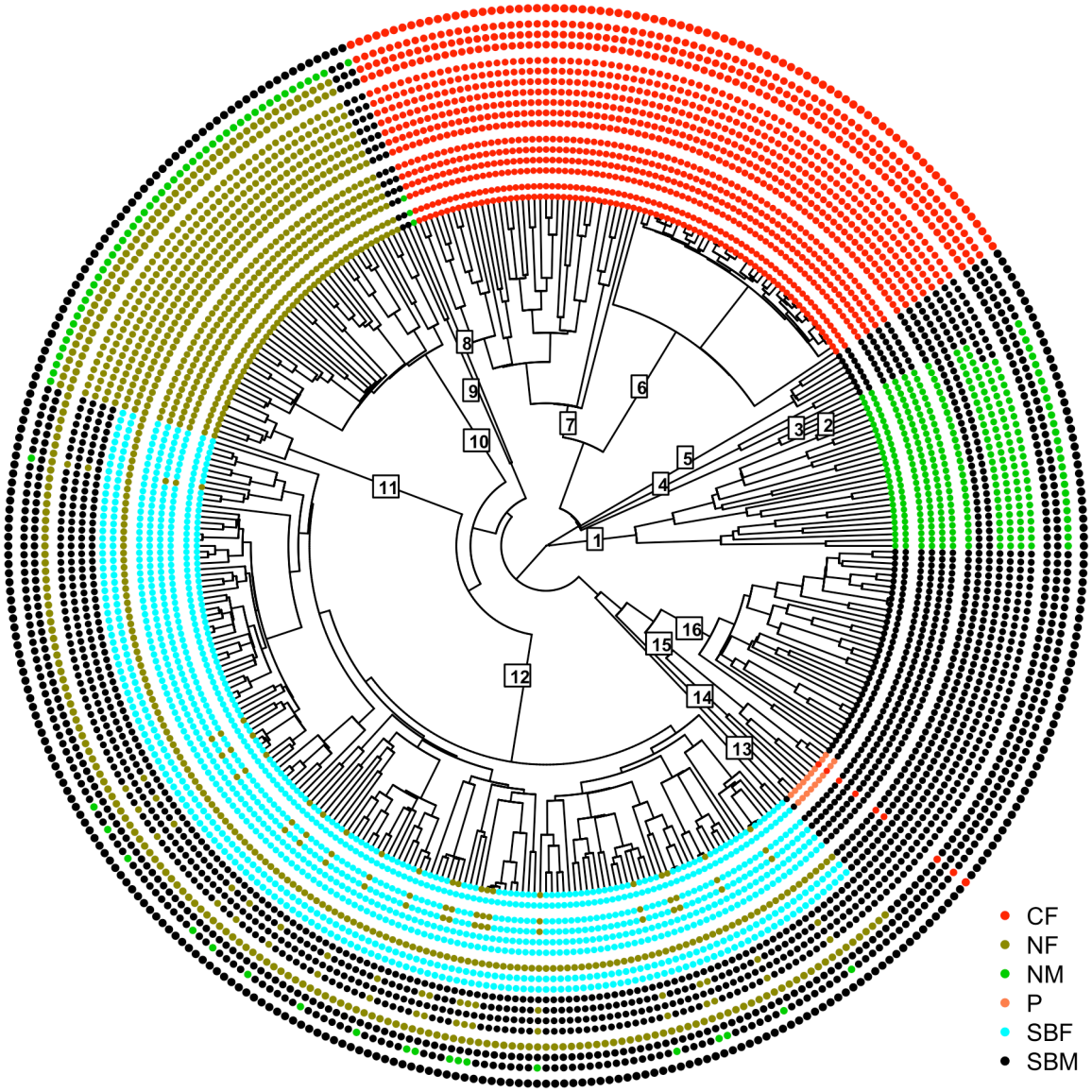


Figure 1: Maximum clade credibility tree depicting the 17 hypothesis of differential rates of evolution across the different types of call structure. The innermost circle depicts the most comprehensive hypothesis, H1, with six rates of evolution, while the other circles represent simplifications of the first scenario. The outermost circle is the hypothesis of two rates, separating HDC and LDC species (H17). Sets of hypotheses are separated with blank spaces according to the number of putative rates (see Tables 1 and 2). Numbers along branches represent the 16 families analyzed: 1-Emballonuridae, 2-Craseonycteridae, 3-Rhinopomatidae, 4-Megadermatidae, 5-Nycteridae, 6-Rhinolophidae, 7-Hipposideridae, 8-Thyropteridae, 9-Natalidae, 10-Molossidae, 11-Miniopteridae, 12-Vespertilionidae, 13-Mystacinidae, 14-Noctilionidae, 15-Mormoopidae, 16-Phyllostomidae. See the supplementary figure S1 for the mappings of each hypothesis into the phylogeny.

Table 1: Call structure classification assumed for each family in the 18 hypotheses of differential rates of phenotypic evolution. The first scenario, BM1, assumes a single rate of evolution for all call types. H1 refers to the six call structures described in Jones & Teeling (2006), while the other hypotheses represent simplifications of this first scenario (see text). See Figure 1 for a graphical representation and characterization of the families with more than one call structure/rate (Vespertilionidae and Mormoopidae).

Family	BM1	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12	H13	H14	H15	H16	H17
Emballonuridae	single	NM	NM	NM	NM	NM	NM	NM	SBM	SBM	NM	NM	NM	NM	SBM	SBM	NM	SBM
Craseonycteridae	single	NM	NM	NM	NM	NM	NM	NM	SBM	SBM	NM	NM	SBM	SBM	SBM	SBM	NM	SBM
Rhinopomatidae	single	NM	NM	NM	NM	NM	NM	NM	SBM	SBM	NM	NM	SBM	SBM	SBM	SBM	NM	SBM
Megadermatidae	single	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM
Nycteridae	single	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM
Rhinolophidae	single	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF
Hipposideridae	single	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF	CF
Thyropteridae	single	NM	NM	NM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	NM	SBM
Natalidae	single	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM
Molossidae	single	NF	NF	NF	NF	NF	NF	NF	NF	NF	NF	NF	NF	NF	NF	NF	NM	SBM
Miniopteridae	single	NF	NF	NF	NF	NF	NF	NF	NF	NF	NF	NF	NF	NF	NF	NF	NM	SBM
Vespertilionidae	single	SBF+ NF	SBF	SBF+ NF	SBF+ NF	SBF	SBF	NF	SBF	SBF	SBM	SBM+ NF	SBM	SBM+ NF	NF	SBM	SBM+ NM	SBM
Mystacinidae	single	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM
Noctilionidae	single	P	P	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM
Mormoopidae	single	P+ CF	P+ CF	SBM+ CF	SBM	SBM+ CF	SBM	SBM+ CF	SBM+ CF	SBM	SBM	SBM	SBM	SBM	SBM+ CF	SBM	SBM+ CF	SBM+ CF
Phyllostomidae	single	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM	SBM

In addition, we used 345 species for which we have data on both FME and forearm length (FA) to evaluate the hypothesis of constrained evolution of echolocation and body size. The same 18 scenarios were evaluated for this purpose with the function `OUwie.joint` (see Leslie *et al.* 2014) from the R package `OUwie`, also considering a Brownian motion model with one or multiple evolutionary rates. In this function, the evolutionary rates in each hypothetical classification can be constrained or not to be equal between the two traits, and AICc (sample size corrected Akaike Information Criterion) values are returned for the constrained and unconstrained scenarios, through which the hypothesis of joint evolution can be compared. For consistency, we repeated all the analyses using FA alone.

In all cases, the function `ace` from the R package `ape` 3.1.4 (Paradis *et al.* 2004) was used to reconstruct the maximum likelihood ancestral states in the internal nodes of the tree (Schluter *et al.* 1997), assuming equal transition rates between states. In all models we used log transformed values of FME and FA. AICc values and the corresponding Akaike weights ($AICc_w$; Burnham & Anderson 2002) were used to compare the fit of the different models. Akaike weights were used to compute weighted averages of the phylogenetic mean values of FME and FA. All analyses were performed in R 3.1.2 (R Core Team 2014).

2.3 Results

The mccTree provides the strongest support to the four-rate model H13 (AIC_w = 0.54; Figure 2; fifth circle from outward in Figure 1), which assigns most vespertilionids, Craseonycteridae and Rhinopomatidae with the same rate as SBM bats. This model also allocates the families Noctilionidae, Thyropteridae and Mormoopidae – including *P. parnellii* – with the same rate as all other Noctilionoidea, SBM. However, the Akaike weights do not unambiguously support it as the best hypothesis (Table 2; see Burnham & Anderson 2002). The four-rate model that assigns all vespertilionids the SBM rate (H12) appears as second best

($AICc_w$ = 0.28) and the model with Craseonycteridae and Rhinopomatidae as NM appears in third (H11, $AICc_w$ = 0.06). The original six-rate model (H1), as well as the simpler two-rate model (H17), shows considerably lower support.

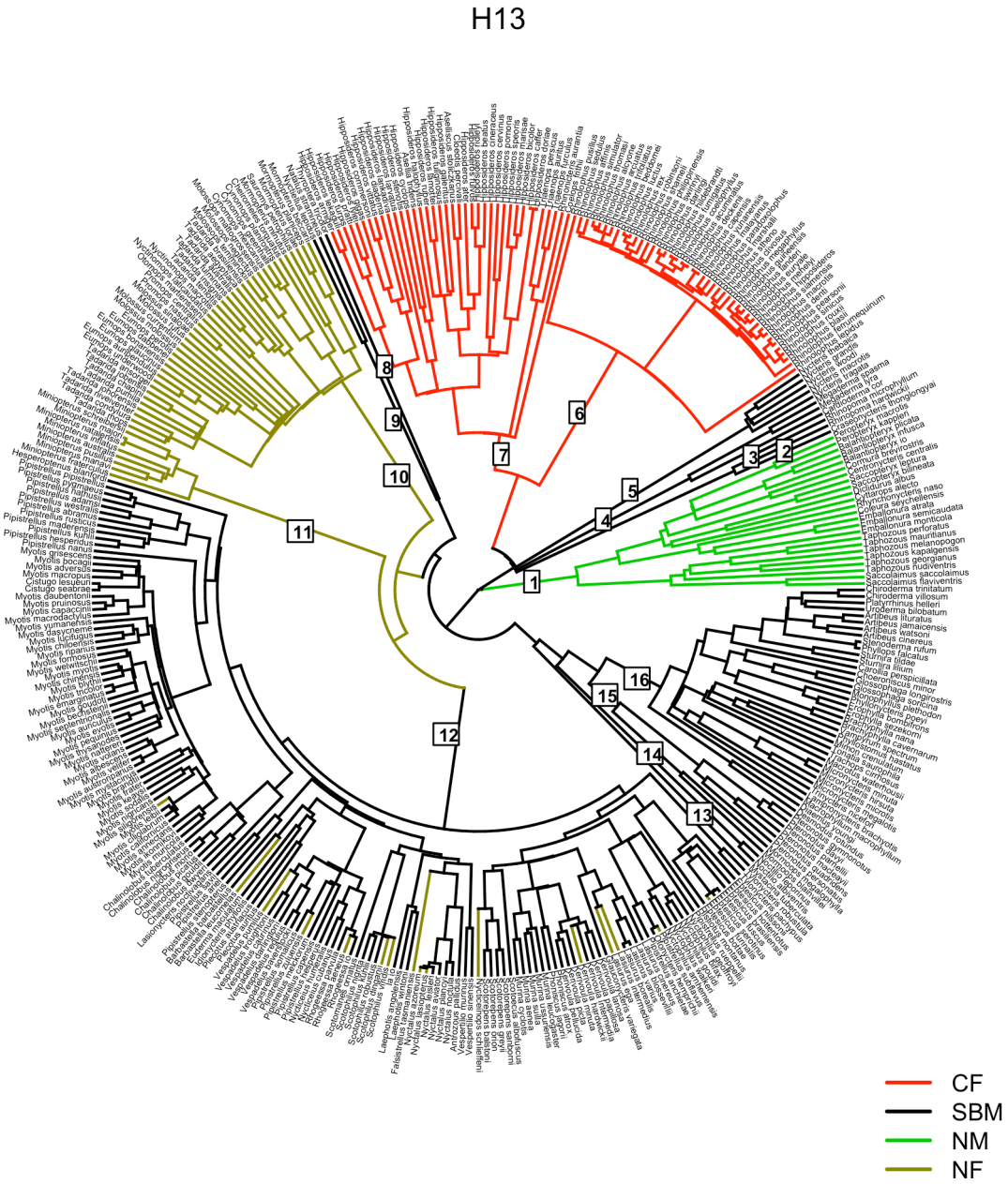


Figure 2: Representation of the hypothesis of differential rates of frequency of maximum energy evolution with greater AICc support, H13. See Figure 1 caption for the family names corresponding to each number along internal branches.

Table 2: Delta AICc and Akaike weights of the 18 models used to evaluate heterogeneity in rates of frequency of maximum energy alone (FME, N = 372 species) and frequency of maximum energy plus forearm length (FME + FA, N = 345), with variable rates between characters (unconstrained) or a common rate between characters (constrained). Δ_{joint} is the AICc of the constrained minus the AICc of the unconstrained models. Models are ordered according to Figure 1, except for the single rate model, BM1, that is not shown in the figure.

Model	Rates	FME		FME + FA unconstrained		FME + FA constrained		Δ_{joint}
		ΔAICc	$AICc_w$	ΔAICc	$AICc_w$	ΔAICc	$AICc_w$	
BM1	1	198.42	0	290.22	0	325.69	0	86.26
H1	6	7.28	0.014	23.74	0	18.91	0	45.96
H2	6	8.09	0.010	18.05	0	18.47	0	51.21
H3	5	7.61	0.012	21.93	0	18.82	0	47.68
H4	5	6.61	0.020	20.86	0	17.3	0	47.23
H5	5	8.68	0.007	16.57	0	18.76	0	52.98
H6	5	7.44	0.013	15.2	0	16.89	0	52.47
H7	4	8.92	0.006	30.24	0	27.27	0	47.82
H8	4	12.13	0.001	17.96	0	22.79	0	55.61
H9	4	10.73	0.003	16.47	0	20.8	0	55.10
H10	4	5.97	0.027	24.66	0	21.52	0	47.65
H11	4	4.38	0.061	16.31	0	14.25	0.001	48.73
H12	4	1.33	0.279	5.36	0.064	5.66	0.056	51.08
H13	4	**0**	**0.543**	**0**	**0.935**	**0**	**0.943**	50.79
H14	3	12.34	0.001	31.66	0	31.26	0	50.38
H15	3	11.89	0.001	34.42	0	33.78	0	50.14
H16	3	14.04	0	39.75	0	37.69	0	48.73
H17	2	12.29	0.001	42.12	0	38.98	0	47.65

Estimated rates for the preferred model show that CF bats have the highest rate of phenotypic evolution, 5.5% greater than the background SBM (1.061 vs. 1.006, Table 3). In all models, NM species appear to have the lowest rate of evolution, except when vespertilionids are all simplified to this category. In models including the polymorphic category, its rate is similar to that of NM species, but there is little support for the differentiation of Mormoopidae and Noctilionidae from the other Noctilionoidea in the models including all species, and even less support when this difference is evaluated only within the superfamily Noctilionoidea (not shown). All ancestral character reconstructions place SBM as the ancestral state for

the echolocating bats, and the best models indicate that most vespertilionids have frequencies of maximum energy that evolve at the same rate of SBM bats, regarding of the ancestral state of Vespertilonoidea being reconstructed as NF. Nevertheless, in the best model, vespertilionids that emit narrowband calls appear to evolve at the same rate as the NF bats in the superfamily Vespertilionoidea.

Table 3: Estimated rates for the three models with higher $AICc_w$, and the originals six-rate and two-rate models of differential rates of evolution of frequency of maximum energy. Numbers in parenthesis are the approximate 95% confidence intervals, calculated according to Beaulieu *et al.* (2012). Blank cells in each model represent classes that were combined with the SBM class. Models are ordered according to $AICc_w$.

Model	**Rates**					
	CF	**NM**	**NF**	**SBF**	**SBM**	**P**
H13	1.061 (1.041-1.080)	1.002 (1.001 – 1.003)	1.010 (1.006 – 1.014)		1.006 (1.005 – 1.008)	
H12	1.061 (1.041-1.080)	1.003 (1.001 – 1.003)	1.005 (1.003 – 1.008)		1.008 (1.006 – 1.009)	
H11	1.061 (1.041-1.080)	1.003 (1.001 – 1.005)	1.010 (1.006 – 1.014)		1.006 (1.005 – 1.008)	
H1	1.060 (1.041-1.079)	1.003 (1.001 – 1.004)	1.010 (1.006 – 1.014)	1.006 (1.004 – 1.008)	1.007 (1.004 – 1.010)	1.003 (1.000 – 1.006)
H17	1.060 (1.041-1.079)				1.007 (1.006 – 1.008)	

The AICc differences between the constrained and unconstrained models show that FME and FA do not evolve at the same rate in any of the evaluated models (Table 2). Both scenarios, however, clearly indicate the H13 also as the best model, with Akaike weights greater than 0.9. As in the case of FME alone, H12 stands as the second best, but in these cases with much lower $AICc_w$ (approximately 0.06 in both scenarios). All unconstrained models show that FA has an overall smaller rate of evolution than FME, majorly for CF and SBM bats (Table 4), and in the constrained scenarios, CF shows a decreased estimate when compared to FME alone, while the other rates appear in the confidence interval estimated for FME rates (Tables 3 and 4). Repeating the analyses with FA alone result in the same models being selected,

with rates identical to those estimated in the unconstrained scenario. This result indicates that frequency of maximum energy and body size evolve in tandem, although with different rates.

Table 4: Estimated rates of evolution of frequency of maximum energy (FME) and forearm length (FA), for the two models with higher $AICc_w$, and the originals six-rate and two-rate models. Unconstrained models estimate separate parameters for FME and FA, while constrained models assume a single rate for both characters. Blank cells in each model represent classes that were combined with the SBM class. Models are ordered according to $AICc_w$.

		Unconstrained models					
Model	**Character**	**CF**	**NM**	**NF**	**SBF**	**SBM**	**P**
H13	FME	1.064	1.002	1.011		1.007	
	FA	1.017	1.001	1.010		1.003	
H12	FME	1.064	1.002	1.006		1.008	
	FA	1.017	1.001	1.002		1.005	
H1	FME	1.063	1.003	1.011	1.006	1.007	1.003
	FA	1.017	1.002	1.009	1.003	1.002	1.003
H17	FME	1.063				1.007	
	FA	1.017				1.004	
		Constrained models					
H13		1.040	1.001	1.010		1.005	
H12		1.040	1.001	1.004		1.006	
H1		1.040	1.002	1.009	1.005	1.005	1.003
H17		1.040				1.005	

The model-averaged phylogenetic mean of FME has a value of 45.32 kHz (SE = 1.23), similar to that estimated by the constrained and unconstrained models (44.69 and 44.76, respectively). Forearm length also has close estimated phylogenetic means between the constrained and unconstrained scenarios, 49.12 and 49.04 mm, respectively.

2.4 Discussion

Echolocation call types are associated with the different habitats in which bats forage, as well as their foraging behaviors (Aldridge & Rautenbach 1987, Schnitzler & Kalko 2001, Schnitzler *et al.* 2003, Denzinger & Schnitzler 2013), leading several authors to suggest the convergence of habitat use and echolocation types among distant bat lineages (Eick *et al.* 2005, Jones & Teeling 2006) due to similar ecological pressures on the evolution of the biosonar. However, we found little support for most hypothesized cases of convergent rates of evolution. The best model allocates 20 species of Vespertilionidae with the same rate as Molossidae and Miniopteridae, and all other species in the family with a reversal to the ancestral rate of echolocating bats, SBM. Moreover, the model simplifying all Vespertilionidae to the same rate cannot be disregarded for FME nor FA, leading to the support of just one case of convergence among all bats. Other echolocation parameters, like bandwidth and call duration, are known to have different structures of phylogenetic dependence (Bilski *et al.* – Chapter 1), and thus can be subject to alternate models of phenotypic evolution.

The preferred model, H13, combines all species that use broadband signals into one single rate. Some vespertilionids that concentrate more energy on the fundamental are known to emit calls with the presence of higher harmonics (Obrist 1995, Jones & Teeling 2006, Fenton *et al.* 2012), and, in some conditions, certain species concentrate more energy on higher harmonics (Bates *et al.* 2011, Fenton *et al.* 2012). Furthermore, H13 includes some species that use narrowband calls with multiple harmonics at the same rate as SBM-SBF bats. These groups live and forage in several disparate conditions, from open xeric habitats in Rhinopomatidae (Qumsiyeh & Jones 1986, Schlitter & Qumsiyeh 1996), up to tropical forests in Thyropteridae and Phyllostomidae (Bernard & Fenton 2002). In addition, Phyllostomidae encompass several dietary patterns besides insectivory (Rojas *et al.* 2011, 2012), although most species are known to consume insects detected through echolocation on an opportunistic manner (Rex *et al.* 2010). Consequently, this grouping cannot be explained by similar environmental or dietary patterns. It is

possible that the grouping of the NM callers simply reflect their difference in relation to the other NM species from Emballonuridae, but a model with a separate rate for these few species would probably generate biased estimates (see O'Meara *et al.* 2006, Beaulieu *et al.* 2012).

The same model selected for FME also explains the variation in FA rates of evolution. This is expected based on the coupling of echolocation modes and frequency with body size (Aldridge & Rautenbach 1987, Norberg & Rayner 1987), and the association of call production with wing beating to diminish the high costs of echolocation (Speakman & Racey 1991, Holderied & von Helversen 2003, Voigt & Lewanzik 2012). The frequency of maximum energy is known to have a negative relation with body size, with larger species emitting lower frequency calls (Jones 1999, Jacobs *et al.* 2007, Bilski *et al.* – Chapter 1). In our results, the highest difference between FME and FA rates is found for CF bats. Several Rhinolophidae species deviate from the allometric scaling between body size and echolocation frequency (Jacobs *et al.* 2007), being the frequencies more closely related to snout length and bite force (Jacobs *et al.* 2014). Moreover, some species in this family are known to adopt a perch-hunting strategy, diminishing their energy requirements (Voigt *et al.* 2010), and perhaps releasing them from the coupling between call production and wing beating.

The finding of a smaller rate of phenotypic evolution in broadband callers and accelerated rates in the more derived echolocation modes, highly adapted to prey detection, is consistent with the view that echolocation evolved first as a spatial orientation mechanism and further switched to prey detection (Schnitzler *et al.* 2003). In addition to facilitating navigation in close space (Denzinger & Schnitzler 2013), broadband signals allow the discrimination of prey items at close distances from the background (Siemers & Schnitzler 2004, Schmieder *et al.* 2012), although there are few known broadband callers capable of finding motionless preys on narrow space environments relying just on echolocation (Geipel *et al.* 2013, Denzinger & Schnitzler 2013. See also Arlettaz *et al.* 2001). Narrowband callers, on the other hand, locate and capture insects in open habitats only using long range, high intensity echolocation (Siemers *et al.* 2001, Schnitzler *et al.* 2003, Jung *et al.*

2014), whereas the highly specialized HDC species use frequency alterations and Doppler shift compensation to separate echoes from background and fluttering insects in narrow space (Fenton *et al.* 1995, 2012). This is not to say that broadband callers are incapable of tracking prey only through echolocation. Species that occupy more dense habitats are known to be capable of assess prey on open space, often changing the echolocation mode and intensity (Kalko & Schnitzler 1993, Jensen & Miller 1999, Brinkløv *et al.* 2010, Hackett *et al.* 2014); but the converse is not true (Fenton 1990, but see Siemers *et al.* 2001), particularly due to the difficulty of open space species in flying in narrow space (Voigt & Holderied 2011).

Trees resolved through the birth-death method of Kuhn *et al.* (2011) tend to pull the species appearance closer to the present (Figure 3; Kuhn *et al.* 2011). This can lead to biased high rates in one group if it has much shorter branches than the other groups with which it is being compared (Thomas *et al.* 2009). Rhinolophidae has notably smaller branches than the rest of the tree, and is thus probably responsible for the higher rate of FME evolution in HDC bats. However, this group shows several cases of partitioning of the acoustical niche space, with low overlapping of maximum energy frequencies among coexisting species (Heller & von Helversen 1989; Kingston *et al.* 2000) and cases of displacement in limited environments (Russo *et al.* 2007). Therefore, this high rate in HDC bats can be reflecting rapid shifts in echolocation frequency caused by niche partitioning (Heller & von Helversen 1989, Moen & Wiens 2009), or a case of cladogenetic evolution (Pennell *et al.* 2014b).

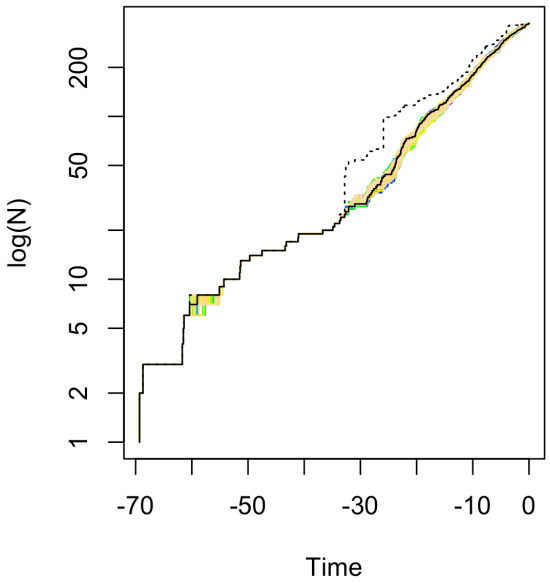


Figure 3: Lineage through time plots for different tree resolutions. Dotted line is the original supertree of Fritz *et al.* (2009); colored lines are 100 polytomy resolutions from Kuhn *et al.* (2011); and the solid black line is the reconstructed maximum clade credibility tree.

The placement of Emballonuridae on the supertree used herein can artificially decrease the rate of evolution in NM compared to SBM. Some molecular phylogenies have put Emballonuridae and Nycteridae (superfamily Emballonuroidea) as sister group of Noctilionoidea and Vespertilionoidea (Eick *et al.* 2005, Teeling *et al.* 2005), with divergence dates around 55 mya, approximately 10 my later than the divergence of Emballonuridae from the other groups in Fritz's *et al.* supertree (although the entire order's dating is shifted towards the present. See also Meredith *et al.* 2011). Rate estimates are proportional to the time of divergence between lineages (Freckleton *et al.* 2002), so the exact placement of a clade in the phylogeny does not affect the calculations, but wrong divergence times often does. By correcting the divergence dates between Emballonuroidae and their sister group, an increase in the rate of evolution for NM can lead it to be in the same range of SBM bats, or even approximate it to the rate of the other species that use narrowband frequencies, but concentrated in the fundamental harmonic (NF). Both scenarios offer interesting interpretations about the rates of evolution in LDC bats:

if NM turns out to be equal to SBM, the only shift in rate from the background SBM would be associated with specializations for long range detection in open space. On the other hand, if NM turns to be equal to NF, the production of a broad frequency spectrum would limit the divergence in FME, irrespective of the number of harmonics present.

A number of other classifications of echolocation types and/or foraging guilds have already been proposed (e.g. Aldridge & Rautenbach 1987, Schnitzler & Kalko 2001, Schnitzler *et al.* 2003, Denzinger & Schnitzler 2013). While some of those have been incorporated and evaluated in our study (H16 is close to Schnitzler's *et al.* 2003), other recent, more complex classifications like Denzinger & Schnitzler's (2013) require a more detailed species level description of habitat use and echolocation characterization. Improving the level of detail in the classification of echolocation types, as well as complete species level phylogenies, can lead to results different from those found herein. However, besides thorough species level characterization, methods capable of confidently pointing rate shifts in small clades have also to be devised (O'Meara *et al.* 2006, Beaulieu *et al.* 2012). We must stress out that our work does not disregard the convergence of echolocation types among distantly related groups (Jones & Teeling 2006, Jones & Holderied 2007), but only points that, in most cases, rates of maximum energy frequency and forearm length evolution are not convergent among groups, still following the rate of phenotypic diversification found in the clades to which they pertain.

2.5 References

Adams, D.C. 2013. Comparing Evolutionary Rates for Different Phenotypic Traits on a Phylogeny Using Likelihood. *Syst. Biol.* **62**: 181–192.

Adams, D.C., Berns, C.M., Kozak, K.H. & Wiens, J.J. 2009. Are rates of species diversification correlated with rates of morphological evolution? *Proc. R. Soc. B Biol. Sci.* **276**: 2729–2738.

Aldridge, H. & Rautenbach, I.L. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. *J. Anim. Ecol.* **56**: 763–778.

Alfaro, M.E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D.L., *et al.* 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc. Natl. Acad. Sci.* **106**: 13410–13414.

Arlettaz, R., Jones, G. & Racey, P.A. 2001. Effect of acoustic clutter on prey detection by bats. *Nature* **414**: 742–745.

Bates, M.E. & Simmons, J.A. 2010. Effects of filtering of harmonics from biosonar echoes on delay acuity by big brown bats (*Eptesicus fuscus*). *J. Acoust. Soc. Am.* **128**: 936–946.

Bates, M.E., Simmons, J.A. & Zorikov, T. V. 2011. Bats Use Echo Harmonic Structure to Distinguish Their Targets from Background Clutter. *Science.* **333**: 627–630.

Beaulieu, J.M., Jhwueng, D.-C., Boettiger, C. & O'Meara, B.C. 2012. Modeling stabilizing selection: expanding the Ornstein-Uhlenbeck model of adaptive evolution. *Evolution.* **66**: 2369–2383.

Bell, G.P. & Fenton, M.B. 1984. The use of Doppler-shifted echoes as a flutter detection and clutter rejection system: the echolocation and feeding behavior of *Hipposideros ruber* (Chiroptera: Hipposideridae). *Behav. Ecol. Sociobiol.* **15**: 109–114.

Bernard, E. & Fenton, M.B. 2002. Species diversity of bats (Mammalia: Chiroptera) in forest fragments, primary forests, and savannas in central Amazonia, Brazil. *Can. J. Zool.* **80**: 1124–1140.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., *et al.* 2007. The delayed rise of present-day mammals. *Nature* **446**: 507–512.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., *et al.* 2008. The delayed rise of present-day mammals (corrigendum). *Nature* **456**: 274.

Boonman, A., Bumrungsri, S. & Yovel, Y. 2014. Nonecholocating Fruit Bats Produce Biosonar Clicks with Their Wings. *Curr. Biol.* **24**: 2962–2967.

Brinkløv, S., Kalko, E. & Surlykke, A. 2010. Dynamic adjustment of biosonar intensity to habitat clutter in the bat *Macrophyllum macrophyllum* (Phyllostomidae). *Behav. Ecol. Sociobiol.* **64**: 1867–1874.

Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media.

Butler, M.A. & King, A.A. 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am. Nat.* **164**: 683–695.

Davis, A.M., Unmack, P.J., Pusey, B.J., Pearson, R.G. & Morgan, D.L. 2014. Evidence for a multi-peak adaptive landscape in the evolution of trophic morphology in terapontid fishes. *Biol. J. Linn. Soc.* **113**: 623–634.

Denzinger, A., Kalko, E.K. V & Jones, G. 2004. Ecological and evolutionary aspects of echolocation in bats. In: *Echolocation in bats and dolphins* (J. Thomas, C. F. Moss, & M. Vater, eds), pp. 311–326. The University of Chicago Press.

Denzinger, A. & Schnitzler, H.-U. 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Front. Physiol.* **4**.

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* **29**: 1969–1973.

Eick, G.N., Jacobs, D.S. & Matthee, C.A. 2005. A Nuclear DNA Phylogenetic Perspective on the Evolution of Echolocation and Historical Biogeography of Extant Bats (Chiroptera). *Mol Biol Evol* **22**: 1869–1886.

Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* **125**: 1–15.

Fenton, M.B., Audet, D., Orbrist, M.K. & Rydell, J. 1995. Signal strength, timing, and self-deafening: the evolution of echolocation in bats. *Paleobiology* **21**: 229–242.

Fenton, M.B., Faure, P.A. & Ratcliffe, J.M. 2012. Evolution of high duty cycle echolocation in bats. *J. Exp. Biol.* **215**: 2935–2944.

Fenton, M.B. & Ratcliffe, J.M. 2014. Sensory Biology: Echolocation from Click to Call, Mouth to Wing. *Curr. Biol.* **24**: R1160–R1162.

Fenton, M.B., Rydell, J., Vonhof, M.J., Eklöf, J. & Lancaster, W.C. 1999. Constant-frequency and frequency-modulated components in the echolocation calls of three species of small bats (Emballonuridae, Thyropteridae, and Vespertilionidae). *Can. J. Zool.* **77**: 1891–1900.

Freckleton, R.P., Harvey, P.H. & Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**: 712–726.

Fritz, S.A., Bininda-Emonds, O.R.P. & Purvis, A. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* **12**: 538–549.

Geipel, I., Jung, K. & Kalko, E.K. V. 2013. Perception of silent and motionless prey on vegetation by echolocation in the gleaning bat *Micronycteris microtis*. *Proc. R. Soc. B Biol. Sci.* **280**: 20122830.

Griffin, D.R. 1946. Supersonic cries of bats. *Nature* **158**: 46–48.

Griffin, D.R., Webster, F.A. & Michael, C.R. 1960. The echolocation of flying insects by bats. *Anim. Behav.* **8**: 141–154.

Hackett, T.D., Korine, C. & Holderied, M.W. 2014. A whispering bat that screams: bimodal switch of foraging guild from gleaning to aerial hawking in the desert long-eared bat. *J. Exp. Biol.* **217**: 3028–3032.

Hansen, T.F. 1997. Stabilizing selection and the comparative analysis of adaptation. *Evolution.* **51**: 1341–1351.

Hansen, T.F. & Martins, E.P. 1996. Translating between microevolutionary process and macroevolutionary patterns: the correlation structure of interspecific data. *Evolution.* 1404–1417.

Harmon, L.J., Losos, J.B., Jonathan Davies, T., Gillespie, R.G., Gittleman, J.L., Bryan Jennings, W., *et al.* 2010. Early bursts of body size and shape evolution are rare in comparative data. *Evolution.* **64**: 2385–2396.

Harmon, L.J., Melville, J., Larson, A. & Losos, J.B. 2008. The Role of Geography and Ecological Opportunity in the Diversification of Day Geckos (Phelsuma). *Syst. Biol.* **57**: 562–573.

Heller, K.-G. & Helversen, O. v. 1989. Resource partitioning of sonar frequency bands in rhinolophoid bats. *Oecologia* **80**: 178–186.

Ho, L.S.T. & Ané, C. 2014. Intrinsic inference difficulties for trait evolution with Ornstein-Uhlenbeck models. *Methods Ecol. Evol.* **5**: 1133–1146.

Holderied, M.W., Jones, G. & von Helversen, O. 2006. Flight and echolocation behaviour of whiskered bats commuting along a hedgerow: range-dependent sonar signal design, Doppler tolerance and evidence for `acoustic focussing'. *J. Exp. Biol.* **209**: 1816–1826.

Holderied, M.W. & von Helversen, O. 2003. Echolocation range and wingbeat period match in aerial-hawking bats. *Proc. R. Soc. London. Ser. B Biol. Sci.* **270**: 2293–2299.

Jacobs, D., Barclay, R. & Walker, M. 2007. The allometry of echolocation call frequencies of insectivorous bats: why do some species deviate from the pattern? *Oecologia* **152**: 583–594.

Jacobs, D.S., Bastian, A. & Bam, L. 2014. The influence of feeding on the evolution of sensory signals: a comparative test of an evolutionary trade-off between masticatory and sensory functions of skulls in southern African Horseshoe bats (Rhinolophidae). *J. Evol. Biol.* **27**: 2829–2840.

Jakobsen, L., Brinkløv, S. & Surlykke, A. 2013. Intensity and directionality of bat echolocation signals. *Front. Physiol.* **4**.

Jakobsen, L., Ratcliffe, J.M. & Surlykke, A. 2012. Convergent acoustic field of view in echolocating bats. *Nature* **493**: 93-96

Jensen, M.E. & Miller, L.A. 1999. Echolocation signals of the bat *Eptesicus serotinus* recorded using a vertical microphone array: effect of flight altitude on searching signals. *Behav. Ecol. Sociobiol.* **47**: 60–69.

Jones, G. 1999. Scaling of echolocation call parameters in bats. *J Exp Biol* **202**: 3359–3367.

Jones, G. & Holderied, M.W. 2007. Bat echolocation calls: adaptation and convergent evolution. *Proc. R. Soc. B Biol. Sci.* **274**: 905–912.

Jones, G. & Teeling, E.C. 2006. The evolution of echolocation in bats. *Trends Ecol. Evol.* **21**: 149–156.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., *et al.* 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**: 2648.

Jung, K., Kalko, E.K. V & Von Helversen, O. 2007. Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *J. Zool.* **272**: 125–137.

Jung, K., Molinari, J. & Kalko, E.K. V. 2014. Driving Factors for the Evolution of Species-Specific Echolocation Call Design in New World Free-Tailed Bats (Molossidae). *PLoS One* **9**: e85279.

Kaliontzopoulou, A., Carretero, M.A. & Adams, D.C. 2015. Ecomorphological variation in male and female wall lizards and the macroevolution of sexual dimorphism in relation to habitat use. *J. Evol. Biol.* **28**: 80–94.

Kalko, E.K. V & Schnitzler, H.U. 1993. Plasticity in echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection. *Behav. Ecol. Sociobiol.* **33**: 415–428.

Kalko, E.K. V & Schnitzler, H.U. 1989. The echolocation and hunting behavior of Daubenton's bat, *Myotis daubentoni*. *Behav. Ecol. Sociobiol.* **24**: 225–238.

Kingston, T., Jones, G., Zubaid, A. & Kunz, T.H. 2000. Resource partitioning in rhinolophoid bats revisited. *Oecologia* **124**: 332–342.

Korine, C. & Kalko, E. 2005. Fruit detection and discrimination by small fruit-eating bats (Phyllostomidae): echolocation call design and olfaction. *Behav. Ecol. Sociobiol.* **59**: 12–23.

Koselj, K., Schnitzler, H.-U. & Siemers, B.M. 2011. Horseshoe bats make adaptive prey-selection decisions, informed by echo cues. *Proc. R. Soc. B Biol. Sci.* **278**: 3034–3041.

Kuhn, T.S., Mooers, A.Ø. & Thomas, G.H. 2011. A simple polytomy resolver for dated phylogenies. *Methods Ecol. Evol.* **2**: 427-436.

Lawrence, B.D. & Simmons, J.A. 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J. Acoust. Soc. Am.* **71**: 585–590.

Leslie, A.B., Beaulieu, J.M., Crane, P.R. & Donoghue, M.J. 2014. Cone size is related to branching architecture in conifers. *New Phytol.* **203**: 1119–1127.

Losos, J.B. & Miles, D.B. 2002. Testing the hypothesis that a clade has adaptively radiated: iguanid lizard clades as a case study. *Am. Nat.* **160**: 147–157.

Mahler, D.L., Revell, L.J., Glor, R.E. & Losos, J.B. 2010. Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. *Evolution.* **64**: 2731–2745.

Maltby, A., Jones, K.E. & Jones, G. 2010. Understanding the evolutionary origin and diversification of bat echolocation. In: *Handbook of mammalian vocalizations and intergrative neuroscience approach* (S. M. Brudzynski, ed), pp. 37–47.

Meredith, R.W., Janečka, J.E., Gatesy, J., Ryder, O.A., Fisher, C.A., Teeling, E.C., *et al.* 2011. Impacts of the Cretaceous Terrestrial Revolution and KPg Extinction on Mammal Diversification. *Science.* **334**: 521–524.

Moen, D.S. & Wiens, J.J. 2009. Phylogenetic evidence for competitively driven divergence: body-size evolution in Caribbean treefrogs (Hylidae: Osteopilus). *Evolution.* **63**: 195–214.

Moss, C.F. & Surlykke, A. 2010. Probing the Natural Scene by Echolocation in Bats. *Front. Behav. Neurosci.* **4**. Frontiers Research Foundation.

Neuweiler, G. 1989. Foraging ecology and audition in echolocating bats. *Trends Ecol. Evol.* **4**: 160–166.

Norberg, U.M. 1994. Wing design, flight performance, and habitat use in bats. In: *Ecological morphology: integrative organismal biology* (P. C. Wainwright & S. M. Reilly, eds), pp. 205–239. The University of Chicago Press.

Norberg, U.M. & Rayner, J.M. V. 1987. Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging

Strategy and Echolocation. *Philos. Trans. R. Soc. London. B, Biol. Sci.* **316**: 335–427.

O'Meara, B.C., Ané, C., Sanderson, M.J., Wainwright, P.C. & Hansen, T. 2006. Testing for different rates of continuous trait evolution using likelihood. *Evolution (N. Y).* **60**: 922–933.

Obrist, M.K. 1995. Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. *Behav. Ecol. Sociobiol.* **36**: 207–219.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* **401**: 877–884.

Paradis, E., Claude, J. & Strimmer, K. 2004. APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics* **20**: 289–290.

Pennell, M., FitzJohn, R.G., Cornwell, W.K. & Harmon, L.J. 2014. Model adequacy and the macroevolution of angiosperm functional traits. *bioRxiv*, doi: 10.1101/004002.

Pennell, M.W., Harmon, L.J. & Uyeda, J.C. 2014. Is there room for punctuated equilibrium in macroevolution? *Trends Ecol. Evol.* **29**: 23–32.

Puttick, M.N., Thomas, G.H. & Benton, M.J. 2014. High rates of evolution preceded the origin of birds. *Evolution (N. Y).* **68**: 1497–1510.

Qumsiyeh, M.B. & Jones, J.K. 1986. *Rhinopoma hardwickii* and *Rhinopoma muscatellum*. *Mamm. Species* 1–5.

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Rabosky, D.L. & Lovette, I.J. 2008. Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? *Evolution.* **62**: 1866–1875.

Rex, K., Czaczkes, B.I., Michener, R., Kunz, T.H. & Voigt, C.C. 2010. Specialization and Omnivory in Diverse Mammalian Assemblages. *Ecoscience* **17**: 37–46.

Rojas, D., Vale, Á., Ferrero, V. & Navarro, L. 2012. The role of frugivory in the diversification of bats in the Neotropics. *J. Biogeogr.* **39**: 1948-1960

Rojas, D., Vale, Á., Ferrero, V. & Navarro, L. 2011. When did plants become important to leaf-nosed bats? Diversification of feeding habits in the family Phyllostomidae. *Mol. Ecol.* **27**: 2217-2228

Russo, D., Mucedda, M., Bello, M., Biscardi, S., Pidinchedda, E. & Jones, G. 2007. Divergent echolocation call frequencies in insular rhinolophids (Chiroptera): a case of character displacement? *J. Biogeogr.* **34**: 2129–2138.

Schlitter, D.A. & Qumsiyeh, M.B. 1996. *Rhinopoma microphyllum*. *Mamm. Species* 1–5.

Schluter, D., Price, T., Mooers, A.Ø. & Ludwig, D. 1997. Likelihood of ancestor states in adaptive radiation. *Evolution.* 1699–1711.

Schmieder, D.A., Kingston, T., Hashim, R. & Siemers, B.M. 2012. Sensory constraints on prey detection performance in an ensemble of vespertilionid understorey rain forest bats. *Funct. Ecol.* **26**: 1043-1053.

Schnitzler, H.-U., Moss, C.F. & Denzinger, A. 2003. From spatial orientation to food acquisition in echolocating bats. *Trends Ecol. Evol.* **18**: 386–394.

Schnitzler, H.U. & Kalko, E.K. V. 2001. Echolocation by insect-eating bats. *Bioscience* **51**: 557–569.

Schnitzler, H.U. & Kalko, E.K. V. 1998. How echolocating bats search and find food. In: *Bat biology and conservation* (T. H. Kunz & P. A. Racey, eds), pp. 183–196. Smithsonian Institution Press, Washington, DC

Schuller, G. & Moss, C.F. 2004. Vocal control and acoustically guided behavior in bats. In: *Echolocation in bats and dolphins* (J. Thomas, C. F. Moss, & M. Vater, eds), pp. 3–16. The University of Chicago Press.

Siemers, B., Kalko, E. & Schnitzler, H.-U. 2001. Echolocation behavior and signal plasticity in the Neotropical bat *Myotis nigricans* (Schinz, 1821) (Vespertilionidae): a convergent case with European species of Pipistrellus? *Behav. Ecol. Sociobiol.* **50**: 317–328.

Siemers, B.M. & Schnitzler, H.-U. 2004. Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature* **429**: 657–661.

Simmons, N.B. 2005. An Eocene Big Bang for Bats. *Science.* **307**: 527–528.

Speakman, J.R. 1993. The evolution of echolocation for predation. In: *Symposia of the Zoological Society of London*, pp. 39–63.

Speakman, J.R., Anderson, M.E. & Racey, P.A. 1989. The energy cost of echolocation in pipistrelle bats (*Pipistrettus pipistrellus*). *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **165**: 679–685.

Speakman, J.R. & Racey, P.A. 1991. No cost of echolocation for bats in flight. *Nature* **350**: 421–423.

Surlykke, A. & Kalko, E.K. V. 2008. Echolocating Bats Cry Out Loud to Detect Their Prey. *PLoS One* **3**: e2036.

Teeling, E.C. 2009. Hear, hear: the convergent evolution of echolocation in bats? *Trends Ecol. Evol.* **24**: 351–354.

Teeling, E.C., Scally, M., Kao, D.J., Romagnoli, M.L., Springer, M.S. & Stanhope, M.J. 2000. Molecular evidence regarding the origin of echolocation and flight in bats. *Nature* **403**: 188–192.

Teeling, E.C., Springer, M.S., Madsen, O., Bates, P., O'Brien, S.J. & Murphy, W.J. 2005. A Molecular Phylogeny for Bats Illuminates Biogeography and the Fossil Record. *Science.* **307**: 580–584.

Thomas, G.H., Freckleton, R.P. & Székely, T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proc. R. Soc. B Biol. Sci.* **273**: 1619.

Thomas, G.H., Meiri, S. & Phillimore, A.B. 2009. Body size diversification in Anolis: novel environment and island effects. *Evolution.* **63**: 2017–2030.

Voigt, C. & Lewanzik, D. 2012. "No cost of echolocation for flying bats" revisited. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **182**: 831–840.

Voigt, C.C., Schuller, B.-M., Greif, S. & Siemers, B.M. 2010. Perch-hunting in insectivorous Rhinolophus bats is related to the high energy costs of manoeuvring in flight. *J. Comp. Physiol. B* **180**: 1079–1088.

Von der Emde, G. & Schnitzler, H.-U. 1990. Classification of insects by echolocating greater horseshoe bats. *J. Comp. Physiol. A* **167**: 423–430.

Wiens, J.J., Pyron, R.A. & Moen, D.S. 2011. Phylogenetic origins of local-scale diversity patterns and the causes of Amazonian megadiversity. *Ecol. Lett.* **14**: 643–652.

Wilson, D.E. & Reeder, D.M. 2005. *Mammal species of the world. A taxonomic ang geographic reference*, 3rd ed. (D. E. Wilson & D. M. Reeder, eds). Johns Hopkins University Press.

Yoder, J.B., Clancey, E., Des Roches, S., Eastman, J.M., Gentry, L., Godsoe, W., *et al.* 2010. Ecological opportunity and the origin of adaptive radiations. *J. Evol. Biol.* **23**: 1581–1596.

Yovel, Y., Falk, B., Moss, C.F. & Ulanovsky, N. 2010. Optimal Localization by Pointing Off Axis. *Science.* **327**: 701–704.

2.6 Supplementary material

Table S1: Number of species per family included in the dataset, and the respective number of species described for each family, based on Wilson & Reeder 2005. Note that we follow Miller-Butterworth *et al.* 2007 in recognizing Miniopteridae as a distinct family.

Family	N dataset	Number of species
Craseonycteridae	1	1
Emballonuridae	24	52
Furipteridae	0	2
Hipposideridae	38	85
Megadermatidae	3	5
Miniopteridae	8	24
Molossidae	41	100
Mormoopidae	8	9
Mystacinidae	1	2
Myzopodidae	0	1
Natalidae	2	8
Noctilionidae	2	2
Nycteridae	5	16
Phyllostomidae	37	174
Rhinolophidae	43	77
Rhinopomatidae	2	4
Thyropteridae	1	3
Vespertilionidae	156	392

Table S2: Sources of peak echolocation frequency information for each species. FA represents the species with forearm length information. References are numbered according to the supplementary references list.

Species	FA	References
Craseonycteris thonglongyai	FA	53, 143
Balantiopteryx infusca	FA	59
Balantiopteryx io	FA	59
Balantiopteryx plicata	FA	14, 59, 109
Centronycteris centralis		14, 70
Coleura seychellensis	FA	4, 44
Cormura brevirostris	FA	34, 70
Cyttarops alecto	FA	70
Diclidurus albus	FA	70
Emballonura atrata	FA	78
Emballonura monticola	FA	119
Emballonura semicaudata	FA	46
Peropteryx kappleri	FA	70
Peropteryx macrotis	FA	9, 14 89, 126
Rhynchonycteris naso	FA	33, 105, 118
Saccolaimus flaviventris	FA	93
Saccolaimus saccolaimus	FA	119
Saccopteryx bilineata	FA	9, 70, 88, 89, 105, 118
Saccopteryx leptura	FA	9, 70, 118
Taphozous georgianus	FA	94
Taphozous kapalgensis	FA	94
Taphozous mauritianus	FA	28, 98, 132, 144
Taphozous melanopogon	FA	119, 149
Taphozous nudiventris	FA	8
Taphozous perforatus	FA	7, 8, 34
Asellia tridens	FA	7, 66
Aselliscus stoliczkanus	FA	81, 151
Cloeotis percivali	FA	95, 98, 132, 144
Coelops frithii	FA	151
Hipposideros armiger	FA	56, 117, 151, 155
Hipposideros ater	FA	38
Hipposideros beatus	FA	96
Hipposideros bicolor	FA	23, 56, 76
Hipposideros caffer	FA	95, 98, 132, 144
Hipposideros cervinus	FA	76
Hipposideros cineraceus	FA	22, 56, 76, 117
Hipposideros commersoni	FA	78
Hipposideros cyclops	FA	20
Hipposideros diadema	FA	47, 56, 93
Hipposideros doriae	FA	76
Hipposideros fuliginosus	FA	27
Hipposideros fulvus	FA	76
Hipposideros galeritus	FA	56, 117
Hipposideros gigas	FA	96
Hipposideros halophyllus	FA	22, 56
Hipposideros lamottei	FA	96
Hipposideros lankadiva	FA	108
Hipposideros larvatus	FA	56, 117, 140, 147, 155
Hipposideros lekaguli	FA	56

Hipposideros lylei	FA	140
Hipposideros marisae	FA	96
Hipposideros pomona	FA	23, 117, 140
Hipposideros pratti	FA	151
Hipposideros ridleyi	FA	49, 76
Hipposideros ruber	FA	29, 48, 98
Hipposideros speoris	FA	115
Hipposideros stenotis	FA	93
Hipposideros turpis	FA	56
Hipposideros vittatus		98, 132
Rhinonicteris aurantia	FA	2
Triaenops auritus		78
Triaenops furculus	FA	78
Triaenops persicus	FA	98
Cardioderma cor	FA	19
Megaderma lyra	FA	117, 122
Megaderma spasma	FA	117
Miniopterus australis	FA	38
Miniopterus fraterculus	FA	92, 98, 132
Miniopterus inflatus	FA	98
Miniopterus majori	FA	78, 121
Miniopterus manavi	FA	78, 121
Miniopterus natalensis	FA	92, 98, 132
Miniopterus pusillus	FA	117
Miniopterus schreibersii	FA	107, 111, 125, 132
Cheiromeles torquatus	FA	75
Cynomops greenhalli		71
Cynomops mexicanus		14, 90
Cynomops planirostris	FA	71
Eumops auripendulus	FA	71
Eumops bonariensis	FA	71
Eumops dabbenei		71
Eumops glaucinus	FA	71, 101
Eumops perotis	FA	3
Eumops underwoodi	FA	109
Molossops mattogrossensis	FA	71
Molossops neglectus	FA	71
Molossops temminckii	FA	50, 71
Molossus currentium	FA	71
Molossus molossus	FA	14, 71, 106, 118
Molossus rufus	FA	14, 32, 34, 71, 89, 106
Molossus sinaloae	FA	14, 71, 89, 106, 109
Mormopterus beccarii	FA	93
Mormopterus loriae	FA	93
Mormopterus minutus	FA	100
Mormopterus planiceps	FA	39
Nyctinomops laticaudatus	FA	14, 71, 89
Nyctinomops macrotis	FA	3, 9, 71, 101
Otomops martiensseni	FA	30, 132
Promops centralis	FA	71
Promops nasutus	FA	71
Sauromys petrophilus	FA	131, 132
Tadarida aegyptiaca	FA	30, 131, 132, 144
Tadarida ansorgei	FA	98, 144
Tadarida australis	FA	39, 40

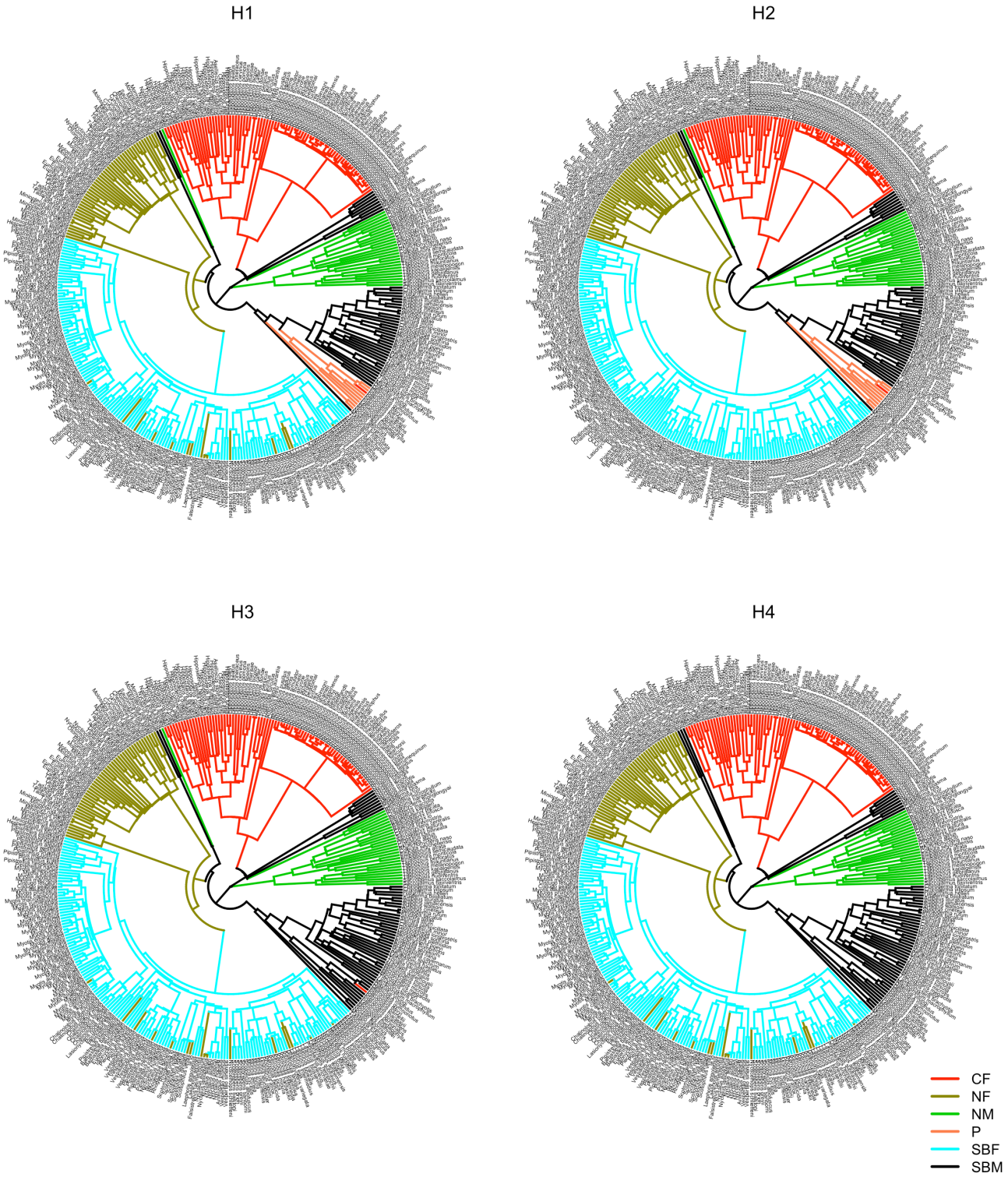
Tadarida brasiliensis	FA	3, 9, 71, 91, 103, 109, 124
Tadarida chapini	FA	144
Tadarida condylura	FA	31, 98, 132, 144
Tadarida fulminans	FA	28
Tadarida insignis		41
Tadarida jobensis	FA	93
Tadarida johorensis	FA	75
Tadarida mops	FA	75
Tadarida niveiventer	FA	132
Tadarida pumila	FA	30, 31, 98, 132, 144
Tadarida teniotis	FA	7, 8, 107, 111, 125
Mormoops blainvillei	FA	65, 85
Mormoops megalophylla	FA	14, 89, 109, 136
Pteronotus davyi	FA	9, 14, 65, 89, 105, 109, 126, 136
Pteronotus gymnonotus	FA	60
Pteronotus macleayii	FA	85
Pteronotus parnellii	FA	14, 65, 85, 89, 105, 109, 126, 136
Pteronotus personatus	FA	14, 89, 90, 105, 109, 136
Pteronotus quadridens	FA	65, 85
Mystacina tuberculata	FA	68, 112, 113
Natalus stramineus	FA	65, 126
Nyctiellus lepidus	FA	103
Noctilio albiventris	FA	55, 73
Noctilio leporinus	FA	14, 106, 130
Nycteris grandis	FA	52, 144
Nycteris macrotis	FA	29, 132
Nycteris thebaica	FA	98, 131, 132, 144
Nycteris tragata	FA	119
Nycteris woodi	FA	144
Artibeus cinereus	FA	118
Artibeus jamaicensis	FA	65, 91, 99, 118
Artibeus lituratus	FA	118
Artibeus watsoni	FA	45, 79
Brachyphylla cavernarum	FA	65
Brachyphylla nana	FA	86
Carollia perspicillata	FA	11, 118, 148
Chiroderma trinitatum	FA	118
Chiroderma villosum	FA	118
Choeroniscus minor	FA	118
Desmodus rotundus	FA	118
Diaemus youngi	FA	17
Erophylla bombifrons	FA	65
Erophylla sezekorni	FA	103
Glossophaga longirostris	FA	65
Glossophaga soricina	FA	118
Lampronycteris brachyotis	FA	118
Macrophyllum macrophyllum	FA	12, 13, 150
Macrotus waterhousii	FA	103
Micronycteris hirsuta	FA	118
Micronycteris megalotis	FA	35, 118
Micronycteris microtis		43
Micronycteris minuta	FA	118
Mimon crenulatum	FA	118
Monophyllus plethodon	FA	65, 91
Phyllonycteris poeyi	FA	99

Phyllops falcatus	FA	87, 99
Phyllostomus hastatus	FA	72, 118
Platyrrhinus helleri	FA	118
Stenoderma rufum	FA	65
Sturnira lilium	FA	65
Sturnira tildae	FA	118
Tonatia saurophila	FA	118
Trachops cirrhosus	FA	6, 47, 142
Trinycteris nicefori	FA	118
Uroderma bilobatum	FA	118
Vampyrum spectrum	FA	118
Rhinolophus acuminatus	FA	56, 76
Rhinolophus affinis	FA	56, 76, 117
Rhinolophus alcyone	FA	27
Rhinolophus arcuatus	FA	133
Rhinolophus beddomei	FA	138
Rhinolophus blasii	FA	8, 62, 98, 111, 132
Rhinolophus capensis	FA	62, 132
Rhinolophus clivosus	FA	7, 8, 62, 98, 131, 132
Rhinolophus coelophyllus	FA	56, 61, 76
Rhinolophus darlingi	FA	62, 98, 132
Rhinolophus deckenii	FA	97, 98
Rhinolophus denti	FA	62, 132
Rhinolophus euryale	FA	111, 125, 127
Rhinolophus ferrumequinum	FA	8, 36, 41, 83, 107, 111, 114, 123, 125, 141
Rhinolophus fumigatus	FA	62, 97, 132
Rhinolophus guineensis	FA	27
Rhinolophus hildebrandti	FA	62, 76, 98, 132
Rhinolophus hipposideros	FA	7, 76, 107, 111, 114, 123, 125
Rhinolophus landeri	FA	27, 29, 62, 76, 97, 132
Rhinolophus lepidus	FA	56, 76, 119
Rhinolophus luctus	FA	56, 76, 119, 151
Rhinolophus macrotis	FA	76
Rhinolophus malayanus	FA	56, 76, 117, 137
Rhinolophus marshalli	FA	151
Rhinolophus megaphyllus	FA	38
Rhinolophus mehelyi	FA	7, 111, 127
Rhinolophus paradoxolophus	FA	25, 151
Rhinolophus pearsonii	FA	56, 76
Rhinolophus philippinensis	FA	77
Rhinolophus pusillus	FA	56, 76, 117, 151
Rhinolophus rex	FA	151
Rhinolophus robinsoni	FA	56
Rhinolophus rouxii	FA	104
Rhinolophus sedulus	FA	76
Rhinolophus shameli	FA	56, 61, 117
Rhinolophus siamensis		151
Rhinolophus simulator	FA	62, 98, 132
Rhinolophus sinicus	FA	151
Rhinolophus stheno	FA	56, 76, 137, 151
Rhinolophus swinnyi	FA	62, 132
Rhinolophus thomasi		57
Rhinolophus trifoliatus	FA	56, 76, 119
Rhinolophus yunanensis	FA	56, 151
Rhinopoma hardwickii	FA	34

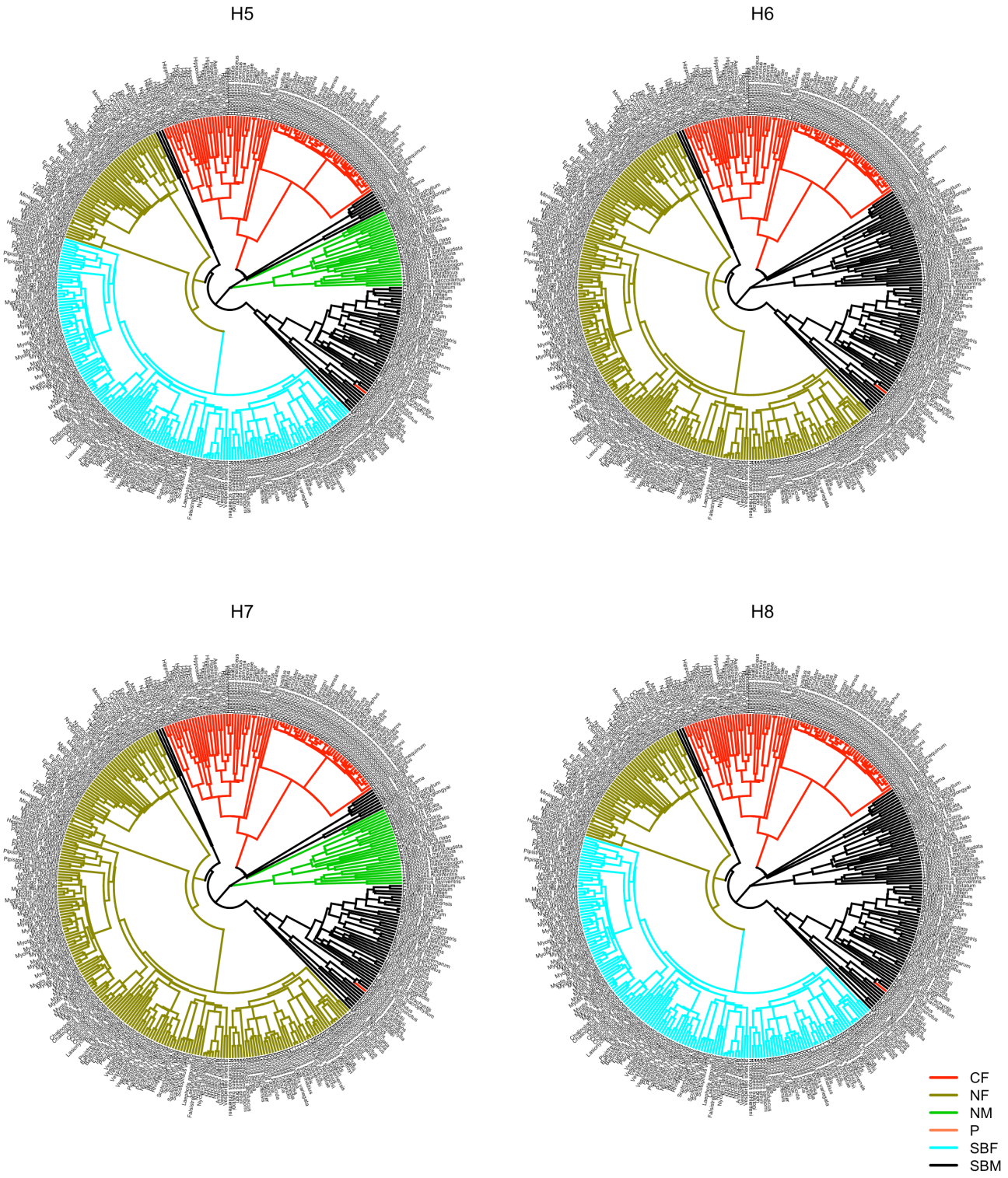
Rhinopoma microphyllum	FA	8, 21
Thyroptera tricolor	FA	33
Antrozous pallidus	FA	28
Barbastella barbastellus	FA	107, 114, 123, 125
Barbastella leucomelas	FA	8
Chalinolobus dwyeri	FA	116
Chalinolobus gouldii	FA	39, 40
Chalinolobus morio	FA	39
Chalinolobus nigrogriseus	FA	93
Chalinolobus picatus	FA	116
Chalinolobus tuberculatus	FA	112, 113
Cistugo lesueuri	FA	131, 132
Cistugo seabrae	FA	132
Eptesicus bottae	FA	7, 8, 54
Eptesicus brasiliensis	FA	118
Eptesicus furinalis	FA	89, 106, 126
Eptesicus fuscus	FA	3, 14, 24, 34, 99, 102
Eptesicus hottentotus	FA	131, 132
Eptesicus nilssonii	FA	36, 107
Eptesicus serotinus	FA	107, 111, 114, 123, 125
Euderma maculatum	FA	37, 80
Falsistrellus tasmaniensis	FA	51, 116
Glauconycteris variegata	FA	132
Hesperoptenus blanfordi	FA	75, 117
Histiotus montanus	FA	124
Ia io	FA	146
Idionycteris phyllotis	FA	135
Kerivoula hardwickii	FA	117
Kerivoula intermedia	FA	74, 129
Kerivoula lanosa	FA	98
Kerivoula minuta	FA	74
Kerivoula papillosa	FA	74, 129
Kerivoula pellucida	FA	74, 129
Kerivoula picta	FA	139
Laephotis angolensis	FA	28
Laephotis wintoni	FA	64, 132
Lasionycteris noctivagans	FA	5, 24, 106
Lasiurus blossevillii	FA	14, 69
Lasiurus borealis	FA	18, 24, 102, 103
Lasiurus cinereus	FA	5, 24, 40, 106
Lasiurus ega	FA	69, 89, 106, 126
Lasiurus intermedius	FA	14, 89, 126
Lasiurus varius		124
Murina aenea	FA	74
Murina cyclotis	FA	74, 129
Murina leucogaster	FA	36, 41, 83, 141
Murina suilla	FA	74, 129
Murina ussuriensis	FA	36, 41
Myotis adversus	FA	40, 119, 134
Myotis albescens	FA	10
Myotis annectans		117
Myotis auriculus	FA	134
Myotis austroriparius	FA	18
Myotis bechsteinii	FA	107, 111, 114, 123, 134
Myotis blythii	FA	107, 111, 125

Pipistrellus abramus	FA	41, 82
Pipistrellus adamsi		93
Pipistrellus anchietae		132
Pipistrellus ariel	FA	7, 8
Pipistrellus capensis		31, 98, 131, 132
Pipistrellus hesperidus		98, 132
Pipistrellus hesperus	FA	47
Pipistrellus kuhlii	FA	8, 107, 111, 125
Pipistrellus maderensis	FA	120, 145
Pipistrellus melckorum		144
Pipistrellus nanus	FA	29, 31, 144
Pipistrellus nathusii	FA	107, 111
Pipistrellus pipistrellus	FA	8, 107, 111, 114, 123, 125, 128
Pipistrellus pygmaeus		207, 111, 114, 123, 125
Pipistrellus rueppellii	FA	28
Pipistrellus rusticus	FA	31, 132, 144
Pipistrellus savii	FA	107, 111, 125
Pipistrellus somalicus		78
Pipistrellus stenopterus	FA	75
Pipistrellus subflavus	FA	18, 24, 84, 102
Pipistrellus westralis		93
Pipistrellus zuluensis		98, 132
Plecotus auritus	FA	107, 123, 125
Plecotus austriacus	FA	107, 111, 120, 125, 145
Rhogeessa aeneus	FA	89, 126
Rhogeessa io	FA	118
Rhogeessa parvula	FA	109
Scotoecus albofuscus	FA	132
Scotomanes ornatus	FA	1
Scotophilus dinganii	FA	63, 98, 132
Scotophilus kuhlii	FA	119
Scotophilus nigrita	FA	28
Scotophilus robustus	FA	78
Scotophilus viridis	FA	31, 98
Scotorepens balstoni	FA	116
Scotorepens greyii	FA	93, 116
Scotorepens orion		116
Scotorepens sanborni	FA	93
Tylonycteris pachypus	FA	117, 152, 153
Tylonycteris robustula	FA	119, 152, 153
Vespadelus baverstocki	FA	116
Vespadelus caurinus		93
Vespadelus darlingtoni	FA	51, 116
Vespadelus pumilus	FA	40
Vespadelus regulus	FA	39
Vespadelus troughtoni		116
Vespertilio murinus	FA	107
Vespertilio sinensis	FA	36, 41

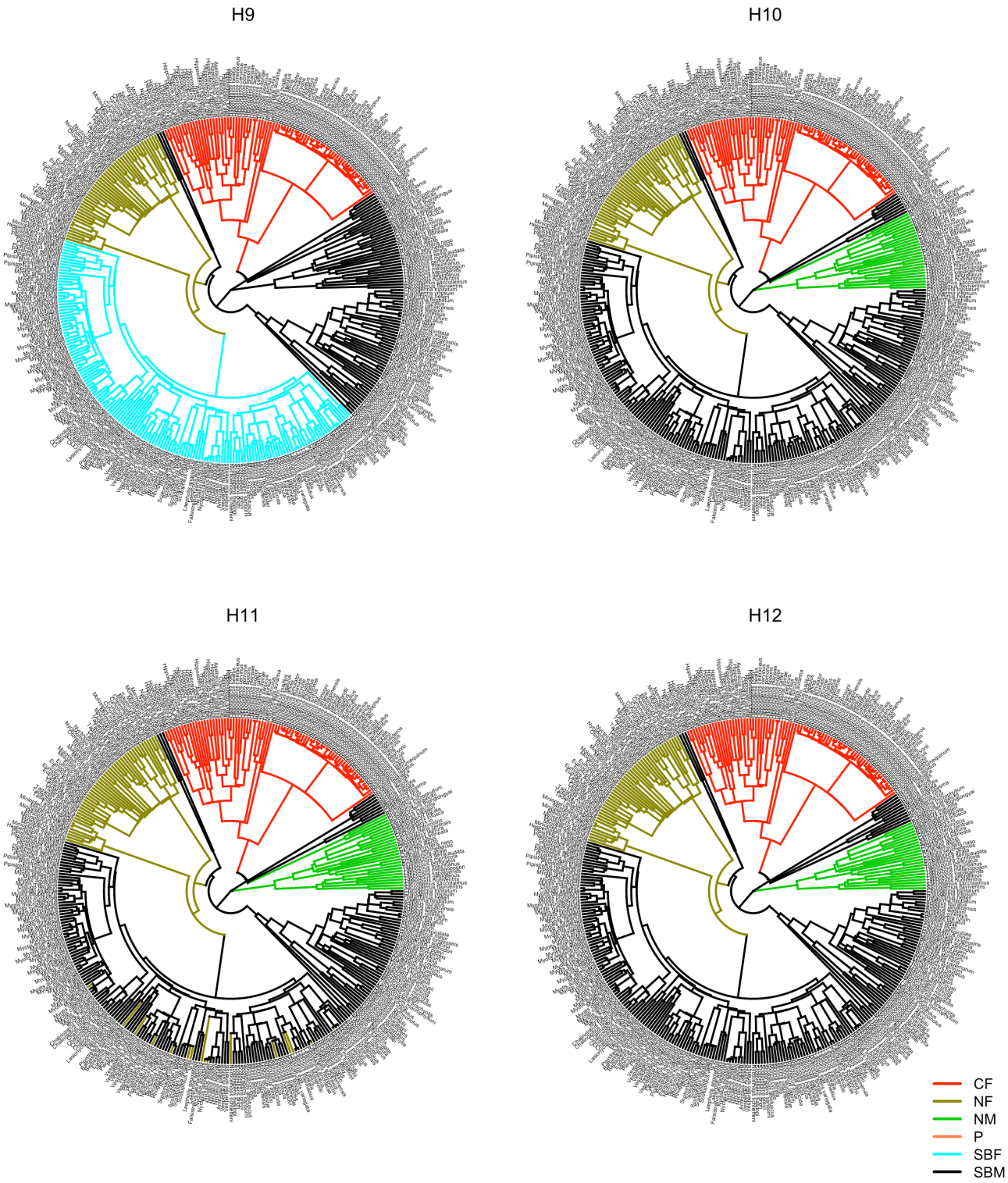
Supporting Figure S1: Evaluated hypotheses of differential rates of peak echolocation frequency and forearm length evolution.



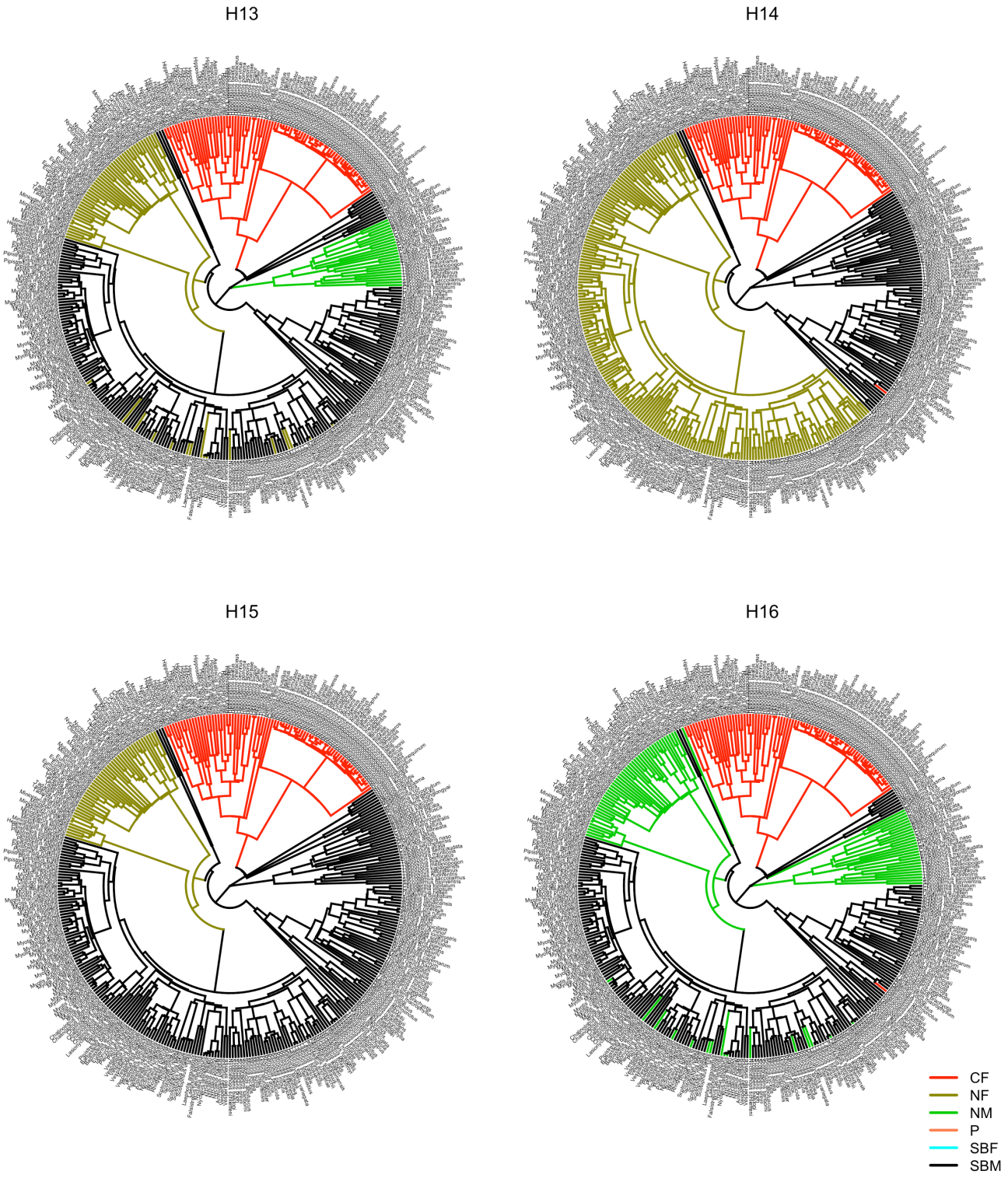
Supporting Figure S1 (continued)



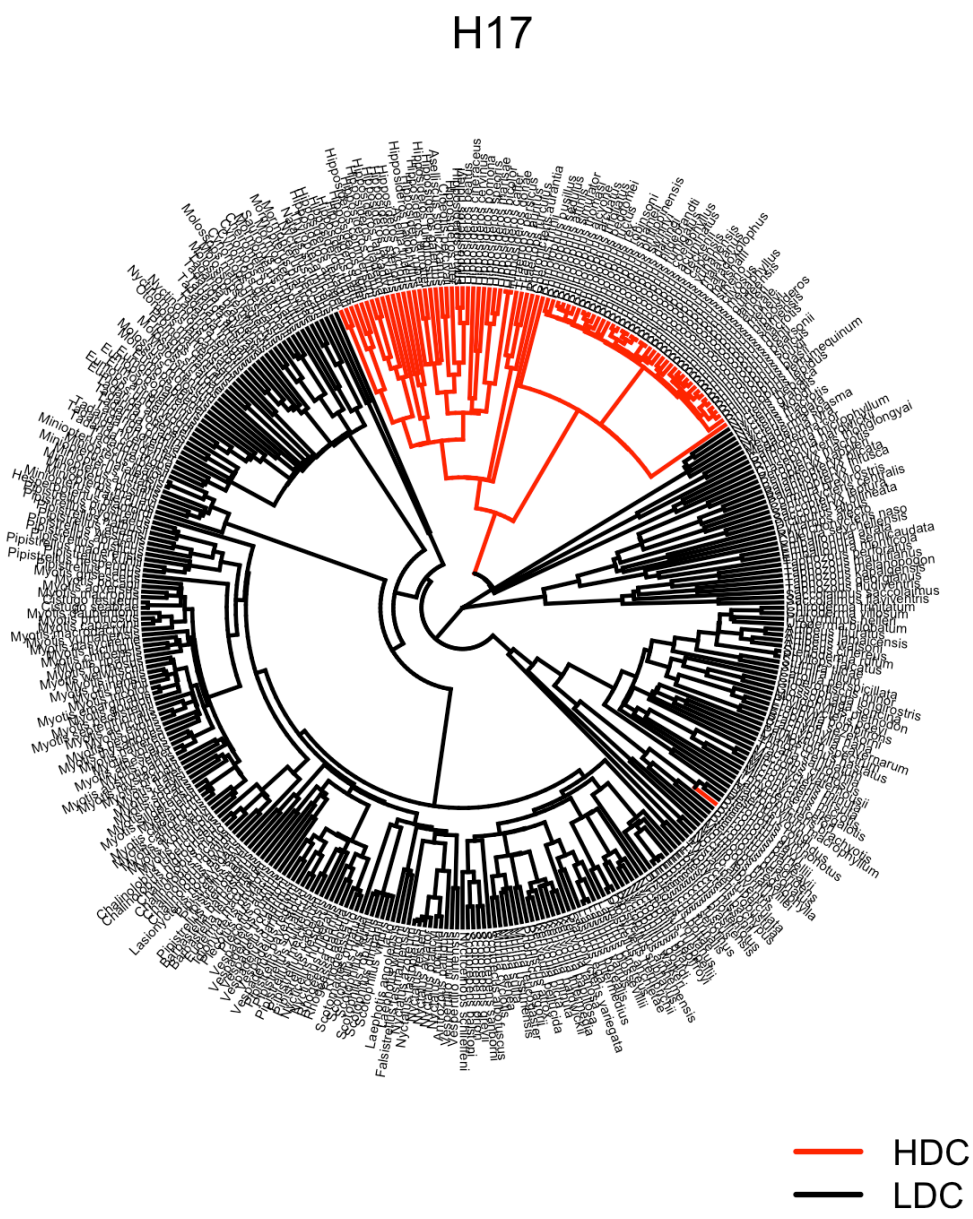
Supporting Figure S1 (continued)



Supporting Figure S1 (continued)



Supporting Figure S1 (continued)



Supplementary references:

1. Abramov, A. V, Kruskop, S. V & Shchinov, A. V. 2010. Small mammals of the Dalat Plateau, southern Vietnam. *Russ. J. Theriol.* **8**: 61–73.

2. Armstrong, K.N. & Coles, R.B. 2007. Echolocation call frequency differences between geographical isolates of Rhinonicteris aurantia (Chiroptera: Hipposideridae): implications of nasal chamber size. *J. Mammal.* **88**: 94–104.

3. Avila-Flores, R. & Fenton, M.B. 2005. Use of spatial features by foraging insectivorous bats in a large urban landscape. *J. Mammal.* **86**: 1193–1204.

4. Bambini, L., Blyth, A., Bradford, T., Bristol, R., Burthe, S., Craig, L., *et al.* 2006. Another Seychelles endemic close to extinction: the emballonurid bat Coleura seychellensis. *Oryx* **40**: 310–318.

5. Barclay, R.M.R. 1986. The echolocation calls of hoary (Lasiurus cinereus) and silver-haired (Lasionycteris noctivagans) bats as adaptations for long- versus short-range foraging strategies and the consequences for prey selection. *Can. J. Zool.* **64**: 2700–2705.

6. Barclay, R.M.R., Fenton, M.B., Tuttle, M.D. & Ryan, M.J. 1981. Echolocation calls produced by Trachops cirrhosus (Chiroptera: Phyllostomatidae) while hunting for frogs. *Can. J. Zool.* **59**: 750–753.

7. Benda, P., Dietz, C., Andreas, M., Hotovy, J., Lucan, R.K., Maltby, A., *et al.* 2008. Bats(Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 6. Bats of Sinai(Egypt) with some taxonomic, ecological and echolocation data on that fauna. *Acta Soc. Zool. Bohemicae* **72**: 1–103.

8. Benda, P., Radek, K.L., Obuch, J., Reiter, A., Andreas, M., Bačkor, P., *et al.* 2010. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 8. Bats of Jordan: fauna, ecology, echolocation, ectoparasites. *Acta Soc. Zool. Bohem* **74**: 185–353.

9. Biscardi, S., Orprecio, J., Fenton, M.B., Tsoar, A. & Ratcliffe, J.M. 2004. Data, sample sizes and statistics affect the recognition of species of bats by their echolocation calls. *Acta chiropterologica* **6**: 347–363.

10. Braun, J.K., Layman, Q.D. & Mares, M.A. 2009. Myotis albescens (Chiroptera: Vespertilionidae). *Mamm. Species* 1–9.

11. Brinkløv, S., Jakobsen, L., Ratcliffe, J.M., Kalko, E.K. V & Surlykke, A. 2011. Echolocation call intensity and directionality in flying short-tailed fruit bats, Carollia perspicillata (Phyllostomidae). *J. Acoust. Soc. Am.* **129**: 427–435.

12. Brinkløv, S., Kalko, E. & Surlykke, A. 2010. Dynamic adjustment of biosonar intensity to habitat clutter in the bat Macrophyllum macrophyllum (Phyllostomidae). *Behav. Ecol. Sociobiol.* **64**: 1867–1874.

13. Brinkløv, S., Kalko, E.K. V & Surlykke, A. 2009. Intense echolocation calls from two `whispering' bats, Artibeus jamaicensis and Macrophyllum macrophyllum (Phyllostomidae). *J. Exp. Biol.* **212**: 11–20.

14. Briones-Salas, M., Peralta-Pérez, M. & García-Luis, M. 2013. Acoustic characterization of new species of bats for the State of Oaxaca, Mexico. *Therya* **4**: 15–32.

15. Britton, A.R.C., Jones, G., Rayner, J.M. V, Boonman, A.M. & Verboom, B. 1997. Flight performance, echolocation and foraging behaviour in pond bats, Myotis dasycneme (Chiroptera: Vespertilionidae). *J. Zool.* **241**: 503–522.

16. Buckley, D.J., Puechmaille, S.J., Roche, N. & Teeling, E.C. 2011. A critical assessment of the presence of Barbastella barbastellus and Nyctalus noctula in Ireland with a description of N. leisleri echolocation calls from Ireland. *Hystrix - Ital. J. Mammal.* **22**: 111–127.

17. Carter, G.G., Fenton, M.B. & Faure, P.A. 2009. White-winged vampire bats (Diaemus youngi) exchange contact calls. *Can. J. Zool.* **87**: 604–608.

18. Corcoran, A.J. 2007. Automated acoustic identification of nine bat species of the eastern United States. Humboldt State University.

19. Csada, R. 1996. Cardioderma cor. *Mamm. Species* 1–4.

20. Decher, J. & Fahr, J. 2005. Hipposideros cyclops. *Mamm. Species* 1–7.

21. Dietz, C. 2005. *Illustrated identification key to the bats of Egypt*.

22. Douangboubpha, B., Bumrungsri, S., Soisook, P., Murray, S.W., Puechmaille, S.J., Satasook, C., *et al.* 2010. A Taxonomic Review of Hipposideros halophyllus, with Additional Information on H. ater and H. cineraceus (Chiroptera: Hipposideridae) from Thailand and Myanmar. *Acta Chiropterologica* **12**: 29–50.

23. Douangboubpha, B., Bumrungsri, S., Soisook, P., Satasook, C., Thomas, N.M. & Bates, P.J.J. 2010. A Taxonomic Review of the Hipposideros bicolor Species Complex and H. pomona (Chiroptera: Hipposideridae) in Thailand. *Acta Chiropterologica* **12**: 415–438.

24. Dzal, Y., Hooton, L.A., Clare, E.L. & Fenton, M.B. 2009. Bat Activity and Genetic Diversity at Long Point, Ontario, an Important Bird Stopover Site. *Acta Chiropterologica* **11**: 307–315.

25. Eger, J.L. & Fenton, M.B. 2003. Rhinolophus paradoxolophus. *Mamm. species* 1–4.

26. Estók, P. & Siemers, B.M. 2009. Calls of a Bird-Eater: The Echolocation Behaviour of the Enigmatic Greater Noctule, Nyctalus lasiopterus. *Acta Chiropterologica* **11**: 405–414.

27. Fahr, J. & Ebigbo, N.M. 2003. A conservation assessment of the bats of the Simandou Range, Guinea, with the first record of Myotis welwitschii (Gray, 1866) from West Africa. *Acta Chiropterologica* **5**: 125–141.

28. Fenton, M.B. & Bell, G.P. 1981. Recognition of species of insectivorous bats by their echolocation calls. *J. Mammal.* 233–243.

29. Fenton, M.B. & Fullard, J.H. 1979. The influence of moth hearing on bat echolocation strategies. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **132**: 77–86.

30. Fenton, M.B., Jacobs, D.S., Richardson, E.J., Taylor, P.J. & White, W. 2004. Individual signatures in the frequency-modulated sweep calls of African large-eared, free-tailed bats Otomops martiensseni (Chiroptera: Molossidae). *J. Zool.* **262**: 11–19.

31. Fenton, M.B., Portfors, C. V, Rautenbach, I.L. & Waterman, J.M. 1998. Compromises: Sound frequencies used in echolocation by aerial-feeding bats. *Can. J. Zool.* **76**: 1174–1182.

32. Fenton, M.B., Rautenbach, I.L., Rydell, J., Arita, H.T., Ortega, J., Bouchard, S., *et al.* 1998. Emergence, Echolocation, Diet and Foraging Behavior of Molossus ater (Chiroptera: Molossidae). *Biotropica* **30**: 314–320.

33. Fenton, M.B., Rydell, J., Vonhof, M.J., Eklöf, J. & Lancaster, W.C. 1999. Constant-frequency and frequency-modulated components in the echolocation calls of three species of small bats (Emballonuridae, Thyropteridae, and Vespertilionidae). *Can. J. Zool.* **77**: 1891–1900.

34. Fenton, M.B., Skowronski, M.D., McGuire, L.P. & Faure, P.A. 2011. Variation in the use of Harmonics in the Calls of Laryngeally Echolocating Bats. *Acta Chiropterologica* **13**: 169–178.

35. Fenton, M.B., Whitaker Jr, J.O., Vonhof, M.J., Waterman, J.M., Pedro, W.A., Aguiar, L., *et al.* 1999. The diet of bats from Southeastern Brazil: the relation to echolocation and foraging behaviour. *Rev. Bras. Zool.* **16**: 1081–1085.

36. Fukui, D., Agetsuma, N. & Hill, D.A. 2004. Acoustic Identification of Eight Species of Bat (Mammalia: Chiroptera) Inhabiting Forests of Southern Hokkaido, Japan: Potential for Conservation Monitoring. *Zoolog. Sci.* **21**: 947–955.

37. Fullard, J. & Dawson, J. 1997. The echolocation calls of the spotted bat Euderma maculatum are relatively inaudible to moths. *J. Exp. Biol.* **200**: 129.

38. Fullard, J.H., Jackson, M.E., Jacobs, D.S., Pavey, C.R. & Burwell, C.J. 2008. Surviving cave bats: auditory and behavioural defences in the Australian noctuid moth, Speiredonia spectans. *J. Exp. Biol.* **211**: 3808–3815.

39. Fullard, J.H., Koehler, C., Surlykke, A. & McKenzie, N.L. 1991. Echolocation ecology and flight morphology of insectivorous bats (Chiroptera) in south-western Australia. *Aust. J. Zool.* **39**: 427–438.

40. Fullard, J.H., Ratcliffe, J.M. & Guignion, C. 2005. Sensory ecology of predator-prey interactions: responses of the AN2 interneuron in the field cricket, Teleogryllus oceanicus to the echolocation calls of sympatric bats. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **191**: 605–618.

41. Funakoshi, K. 2010. Acoustic identification of thirteen insectivorous bat species from the Kyushu District, Japan. *Mamm.* **50**: 165–175.

42. Gannon, W.L., Sherwin, R.E., de Carvalho, T.N. & O'Farrell, M.J. 2001. Pinnae and echolocation call differences between Myotis californicus and M. ciliolabrum (Chiroptera: Vespertilionidae). *Acta chiropterologica* **3**: 77–91.

43. Geipel, I., Jung, K. & Kalko, E.K. V. 2013. Perception of silent and motionless prey on vegetation by echolocation in the gleaning bat Micronycteris microtis. *Proc. R. Soc. B Biol. Sci.* **280**.

44. Gerlach, J. 2008. Vocalisations of the Seychelles sheath-tailed bat Coleura seychellensis. *Le Rhinolophe* **18**: 17–24.

45. Gillam, E.H., Chaverri, G., Montero, K. & Sagot, M. 2013. Social Calls Produced within and near the Roost in Two Species of Tent-Making Bats, Dermanura watsoni and Ectophylla alba. *PLoS One* **8**: e61731.

46. Gorresen, P.M., Bonaccorso, F.J. & Pinzari, C.A. 2009. Habitat Occupancy and Detection of the Pacific Sheath-Tailed Bat (Emballonura semicaudata) on Aguiguan, Commonwealth of the Northern Mariana Islands. *Acta Chiropterologica* **11**: 331–342.

47. Goudy-Trainor, A. & Freeman, P.W. 2002. Call parameters and facial features in bats: a surprising failure of form following function. *Pap. Nat. Resour.* 18.

48. Guillén, A., Juste, B. & Ibáñez, C. 2000. Variation in the frequency of the echolocation calls of Hipposideros ruber in the Gulf of Guinea: an exploration of the adaptive meaning of the constant frequency value in rhinolophoid CF bats. *J. Evol. Biol.* **13**: 70–80.

49. Guillén-Servent, A. & Francis, C.M. 2006. A new species of bat of the Hipposideros bicolor group (Chiroptera: Hipposideridae) from Central Laos, with evidence of convergent evolution with Sundaic taxa. *Acta Chiropterologica* **8**: 39–61.

50. Guillén-Servent, A. & Ibáñez, C. 2007. Unusual echolocation behavior in a small molossid bat, Molossops temminckii, that forages near background clutter. *Behav. Ecol. Sociobiol.* **61**: 1599–1613.

51. Herr, A. 1998. Aspects of the ecology of insectivorous forest-dwelling bats (Microchiroptera) in the western slopes of the Australian alps. Charles Sturt University.

52. Hickey, M.B.C. & Dunlop, J.M. 2000. Nycteris grandis. *Mamm. Species* 1–4.

53. Hill, J.E. & Smith, S.E. 1981. Craseonycteris thonglongyai. *Mamm. species* 1–4.

54. Holderied, M.W., Korine, C., Fenton, M.B., Parsons, S., Robson, S. & Jones, G. 2005. Echolocation call intensity in the aerial hawking bat Eptesicus bottae (Vespertilionidae) studied using stereo videogrammetry. *J. Exp. Biol.* **208**: 1321–1327.

55. Hood, C.S. & Pitocchelli, J. 1983. Noctilio albiventris. *Mamm. Species* 1–5.

56. Hughes, A.C., Satasook, C., Bates, P.J.J., Soisook, P., Sritongchuay, T., Jones, G., *et al.* 2010. Echolocation Call Analysis and Presence-Only Modelling as Conservation Monitoring Tools for Rhinolophoid Bats in Thailand. *Acta chiropterologica* **12**: 311–327.

57. Huihua, Z., Shuyi, Z., Mingxue, Z. & Jiang, Z. 2003. Correlations between call frequency and ear length in bats belonging to the families Rhinolophidae and Hipposideridae. *J. Zool.* **259**: 189–195.

58. Ibáñez, C., Juste, J., García-Mudarra, J.L. & Agirre-Mendi, P.T. 2001. Bat predation on nocturnally migrating birds. *Proc. Natl. Acad. Sci.* **98**: 9700–9702.

59. Ibáñez, C., Juste, J., López-Wilchis, R., Albuja V, L., Núñez-Garduño, A. & O'Shea, T.J. 2002. Echolocation of three species of sac-winged bats (Balantiopteryx). *J. Mammal.* **83**: 1049–1057.

60. Ibáñez, C., Lopez-Wilchis, R., Javier, J.B. & León-Galván, M.A. 2000. Echolocation calls and a noteworthy record of Pteronotus gymnonotus (Chiroptera, Mormoopidae) from Tabasco, Mexico. *Southwest. Nat.* **45**: 345–347.

61. Ith, S., Soisook, P., Bumrungsri, S., Kingston, T., Puechmaille, S.J., Struebig, M.J., *et al.* 2011. A Taxonomic Review of Rhinolophus coelophyllus Peters 1867 and R. shameli Tate 1943 (Chiroptera: Rhinolophidae) in Continental Southeast Asia. *Acta Chiropterologica* **13**: 41–59.

62. Jacobs, D., Barclay, R. & Walker, M. 2007. The allometry of echolocation call frequencies of insectivorous bats: why do some species deviate from the pattern? *Oecologia* **152**: 583–594.

63. Jacobs, D.S. & Barclay, R.M.R. 2009. Niche Differentiation in Two Sympatric Sibling Bat Species, Scotophilus Dinganii and Scotophilus Mhlanganii. *J. Mammal.* **90**: 879–887.

64. Jacobs, D.S., Barclay, R.M.R. & Schoeman, M.C. 2005. Foraging and roosting ecology of a rare insectivorous bat species, Laephotis wintoni (Thomas, 1901), Vespertilionidae. *Acta Chiropterologica* **7**: 101–109.

65. Jennings, N. V, Parsons, S., Barlow, K.E. & Gannon, M.R. 2004. Echolocation calls and wing morphology of bats from the West Indies. *Acta chiropterologica* **6**: 75–90.

66. Jones, G., Morton, M., Hughes, P.M. & Budden, R.M. 1993. Echolocation, flight morphology and foraging strategies of some West African hipposiderid bats. *J. Zool.* **230**: 385–400.

67. Jones, G., Parsons, S., Zhang, S., Stadelmann, B., Benda, P. & Ruedi, M. 2006. Echolocation calls, wing shape, diet and phylogenetic diagnosis of the endemic Chinese bat Myotis pequinius. *Acta Chiropterologica* **8**: 451–463.

68. Jones, G., Webb, P.I., Sedgeley, J.A. & O'Donnell, C.F.J. 2003. Mysterious Mystacina: how the New Zealand short-tailed bat (Mystacina tuberculata) locates insect prey. *J. Exp. Biol.* **206**: 4209–4216.

69. Jung, K. & Kalko, E.K. V. 2011. Adaptability and vulnerability of high flying Neotropical aerial insectivorous bats to urbanization. *Divers. Distrib.* **17**: 262–274.

70. Jung, K., Kalko, E.K. V & Von Helversen, O. 2007. Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *J. Zool.* **272**: 125–137.

71. Jung, K., Molinari, J. & Kalko, E.K. V. 2014. Driving Factors for the Evolution of Species-Specific Echolocation Call Design in New World Free-Tailed Bats (Molossidae). *PLoS One* **9**: e85279.

72. Kalko, E.K. V & Condon, M.A. 1998. Echolocation, olfaction and fruit display: how bats find fruit of flagellichorous cucurbits. *Funct. Ecol.* **12**: 364–372.

73. Kalko, E.K. V, Schnitzler, H.U., Kaipf, I. & Grinnell, A.D. 1998. Echolocation and foraging behavior of the lesser bulldog bat, Noctilio albiventris: preadaptations for piscivory? *Behav. Ecol. Sociobiol.* **42**: 305–319.

74. Kingston, T., Jones, G., Akbar, Z. & Kunz, T.H. 1999. Echolocation signal design in Kerivoulinae and Murininae (Chiroptera: Vespertilionidae) from Malaysia. *J. Zool.* **249**: 359–374.

75. Kingston, T., Jones, G., Akbar, Z., Kunz, T.H. & O'Shea, T.J. 2003. Alternation of echolocation calls in 5 species of aerial-feeding insectivorous bats from Malaysia. *J. Mammal.* **84**: 205–215.

76. Kingston, T., Jones, G., Zubaid, A. & Kunz, T.H. 2000. Resource partitioning in rhinolophoid bats revisited. *Oecologia* **124**: 332–342.

77. Kingston, T. & Rossiter, S.J. 2004. Harmonic-hopping in Wallacea's bats. *Nature* **429**: 654–657.

78. Kofoky, A.F., Randrianandrianina, F., Russ, J., Raharinantenaina, I., Cardiff, S.G., Jenkins, R.K.B., *et al.* 2009. Forest Bats of Madagascar: Results of Acoustic Surveys. *Acta Chiropterologica* **11**: 375–392.

79. Korine, C. & Kalko, E. 2005. Fruit detection and discrimination by small fruit-eating bats (Phyllostomidae): echolocation call design and olfaction. *Behav. Ecol. Sociobiol.* **59**: 12–23.

80. Leonard, M.L. & Fenton, M.B. 1984. Echolocation calls of Euderma maculatum (Vespertilionidae): use in orientation and communication. *J. Mammal.* **65**: 122–126.

81. Li, G., Liang, B., Wang, Y., Zhao, H., Helgen, K.M., Lin, L., *et al.* 2007. Echolocation Calls, Diet, and Phylogenetic Relationships of Stoliczka's Trident Bat, Aselliscus stoliczkanus (Hipposideridae). *J. Mammal.* **88**: 736–744.

82. Luo, F., Ma, J., Li, A., Wu, F.J., Chen, Q.C. & Zhang, S.Y. 2007. Echolocation Calls and Neurophysiological Correlations with Auditory Response Properties in the Inferior Colliculus of Pipistrellus abramus(Microchiroptera: Vespertilionidae). *Zool. Stud.* **46**: 622–630.

83. Ma, J., Liang, B., Zhang, S. & Metzner, W. 2008. Dietary composition and echolocation call design of three sympatric insectivorous bat species from China. *Ecol. Res.* **23**: 113–119.

84. MacDonald, K., Matsui, E., Stevens, R. & Fenton, M.B. 1994. Echolocation calls and field identification of the eastern pipistrelle (Pipistrellus subflavus: Chiroptera: Vespertilionidae), using ultrasonic bat detectors. *J. Mammal.* **75**: 462–465.

85. Macías, S., Mora, E.C. & García, A. 2006. Acoustic identification of mormoopid bats: a survey during the evening exodus. *J. Mammal.* **87**: 324–330.

86. Macias, S., Mora, E.C., Garcia, A. & Macias, Y. 2006. Echolocation Behavior of Brachyphylla nana (Chiroptera: Phyllostomidae) under Laboratory Conditions. *Caribb. J. Sci.* **42**: 114.

87. Macías, S., Mora, E.C., Koch, C. & Von Helversen, O. 2005. Echolocation behaviour of Phyllops falcatus (Chiroptera: Phyllostomidae): unusual frequency range of the first harmonic. *Acta Chiropterologica* **7**: 275–283.

88. MacSwiney G., M.C., Bolívar Cimé, B., Clarke, F.M. & Racey, P.A. 2009. Insectivorous Bat Activity at Cenotes in the Yucatan Peninsula, Mexico. *Acta Chiropterologica* **11**: 139–147.

89. MacSwiney G., M.C., Clarke, F.M. & Racey, P.A. 2008. What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. *J. Appl. Ecol.* **45**: 1364–1371.

90. MacSwiney, G.M., Bolívar, B., Clarke, F.M. & Racey, Y.P.A. 2006. Nuevos registros de Pteronotus personatus y Cynomops mexicanus (Chiroptera) en el estado de Yucatán, México. *Rev. Mex. Mastozoología* **10**: 102–109.

91. Medina, H., Lacher, T. & Woolley, J. 2011. Characteristics of echolocation calls of bats in Dominica.

92. Miller-Butterworth, C.M., Eick, G., Jacobs, D.S., Schoeman, M.C. & Harley, E.H. 2005. Genetic and phenotypic differences between South African long-fingered bats, with a global Miniopterine phylogeny. *J. Mammal.* **86**: 1121–1135.

93. Milne, D.J. 2006. Habitat relationships, activity patterns and feeding ecology of insectivorous bats of the top end of Australia. James Cook University.

94. Milne, D.J., Reardon, T.B. & Watt, F. 2003. New records for the Arnhem sheathtail bat Taphozous kapalgensis (Chiroptera: Emballonuridae) from voucher specimens and Anabat recordings. *Aust. Zool.* **32**: 439–445.

95. Monadjem, A., Reside, A. & Lumsden, L. 2007. Echolocation calls of rhinolophid and hipposiderid bats in Swaziland. *South African J. Wildl. Res.* **37**: 9–15.

96. Monadjem, A., Richards, L., Taylor, P.J., Denys, C., Dower, A. & Stoffberg, S. 2013. Diversity of Hipposideridae in the Mount Nimba massif, West Africa, and the Taxonomic Status of Hipposideros lamottei. *Acta Chiropterologica* **15**: 341–352.

97. Monadjem, A., Schoeman, M.C., Reside, A., Pio, D. V, Stoffberg, S., Bayliss, J., *et al.* 2010. A Recent Inventory of the Bats of Mozambique with Documentation of Seven New Species for the Country. *Acta Chiropterologica* **12**: 371–391.

98. Monadjem, A., Taylor, P.J., Cotterill, W. & Schoeman, M.C. 2010. *Bats of southern and central Africa: a biogeographic and taxonomic synthesis*. Wits University Press Johannesburg.

99. Mora, E. & Macías, S. 2007. Echolocation calls of Poey's flower bat (Phyllonycteris poeyi) unlike those of other phyllostomids. *Naturwissenschaften* **94**: 380–383.

100. Mora, E.C., Ibáñez, C., Macías, S., Juste, J., López, I. & Torres, L. 2011. Plasticity in the Echolocation Inventory of Mormopterus minutus (Chiroptera, Molossidae). *Acta Chiropterologica* **13**: 179–187.

101. Mora, E.C. & Torres, L. 2008. Echolocation in the Large Molossid Bats Eumops glaucinus and Nyctinomops macrotis. *Zoolog. Sci.* **25**: 6–13.

102. Murray, K.L., Britzke, E.R. & Robbins, L.W. 2001. Variation in search-phase calls of bats. *J. Mammal.* **82**: 728–737.

103. Murray, K.L., Fraser, E., Davy, C., Fleming, T.H. & Fenton, M.B. 2009. Characterization of the Echolocation Calls of Bats from Exuma, Bahamas. *Acta Chiropterologica* **11**: 415–424.

104. Neuweiler, G., Metzner, W., Heilmann, U., Rübsamen, R., Eckrich, M. & Costa, H.H. 1987. Foraging behaviour and echolocation in the rufous horseshoe bat (Rhinolophus rouxi) of Sri Lanka. *Behav. Ecol. Sociobiol.* **20**: 53–67.

105. O'Farrell, M.J. & Miller, B.W. 1997. A new examination of echolocation calls of some neotropical bats (Emballonuridae and Mormoopidae). *J. Mammal.* 954–963.

106. O'Farrell, M.J., Miller, B.W. & Gannon, W.L. 1999. Qualitative identification of free-flying bats using the Anabat detector. *J. Mammal.* **80**: 11–23.

107. Obrist, M.K., Boesch, R. & Flückiger, P.F. 2004. Variability in echolocation call design of 26 Swiss bat species: consequences, limits and options for automated field identification with a synergetic pattern recognition approach. *Mammalia* **68**: 307–322.

108. Obrist, M.K., Fenton, M.B., Eger, J.L. & Schlegel, P.A. 1993. What ears do for bats: a comparative study of pinna sound pressure transformation in chiroptera. *J Exp Biol* **180**: 119–152.

109. Orozco-Lugo, L., Guillén-Servent, A., Valenzuela-Galván, D. & Arita, H.T. 2013. Descripción de los pulsos de ecolocalización de once especies de murciélagos insectívoros aéreos de una selva baja caducifolia en Morelos, México. *Therya* **4**: 33–46.

110. Ossa, G. 2010. Analysis of the echolocation calis and morphometry of a population of Myotis chiloensis (Waterhouse, 1838) from the southern Chilean temperate forest. *Cienc. Inv. Agr* 131–139.

111. Papadatou, E., Butlin, R.K. & Altringham, J.D. 2008. Identification of bat species in Greece from their echolocation calls. *Acta Chiropterologica* **10**: 127–143.

112. Parsons, S. 2001. Identification of New Zealand bats (Chalinolobus tuberculatus and Mystacina tuberculata) in flight from analysis of echolocation calls by artificial neural networks. *J. Zool.* **253**: 447–456.

113. Parsons, S. 1997. Search-phase echolocation calls of the New Zealand lesser short-tailed bat (Mystacina tuberculata) and long-tailed bat (Chalinolobus tuberculatus). *Can. J. Zool.* **75**: 1487–1494.

114. Parsons, S. & Jones, G. 2000. Acoustic identification of twelve species of echolocating bat by discriminant function analysis and artificial neural networks. *J. Exp. Biol.* **203**: 2641–2656.

115. Pavey, C., Grunwald, J.-E. & Neuweiler, G. 2001. Foraging habitat and echolocation behaviour of Schneider's leafnosed bat, Hipposideros speoris, in a vegetation mosaic in Sri Lanka. *Behav. Ecol. Sociobiol.* **50**: 209–218.

116. Pennay, M., Law, B., Reinhold, L., Wales, N.S., Wales, N.S. & Wales, N.S. 2004. *Bat calls of New South Wales: region based guide to the echolocation of microchiropteran bats*. Department of Environment and Conservation.

117. Phauk, S., Phen, S. & Furey, N.M. 2013. Cambodian bat echolocation: a first description of assemblage call param- eters and assessment of their utility for species identification. *Cambodian J. Nat. Hist.* 16–26.

118. Pio, D.V. V, Clarke, F.M., MacKie, I. & Racey, P.A. 2010. Echolocation Calls of the Bats of Trinidad, West Indies: Is Guild Membership Reflected in Echolocation Signal Design? *Acta chiropterologica* **12**: 217–229.

119. Pottie, S.A., Lane, D.J.W., Kingston, T. & Y.-H. Lee, B.P. 2005. The microchiropteran bat fauna of Singapore. *Acta Chiropterologica* **7**: 237–247.

120. Rainho, A., Marques, J. & Palmeirim, J.M. 2002. Os morcegos dos arquipélagos dos Açores e da Madeira: um contributo para a sua conservação. Instituto da Conservação da Natureza, Lisboa.

121. Ramasindrazana, B., Goodman, S.M., Schoeman, M.C. & Appleton, B. 2011. Identification of cryptic species of Miniopterus bats (Chiroptera: Miniopteridae) from Madagascar and the Comoros using bioacoustics overlaid on molecular genetic and morphological characters. *Biol. J. Linn. Soc.* **104**: 284–302.

122. Ratcliffe, J.M., Raghuram, H., Marimuthu, G., Fullard, J.H. & Fenton, M.B. 2005. Hunting in unfamiliar space: echolocation in the Indian false vampire bat, Megaderma lyra, when gleaning prey. *Behav. Ecol. Sociobiol.* **58**: 157–164.

123. Redgwell, R.D., Szewczak, J.M., Jones, G. & Parsons, S. 2009. Classification of echolocation calls from 14 species of bat by support vector machines and ensembles of neural networks. *Algorithms* **2**: 907–924.

124. Rodríguez-San Pedro, A. & Simonetti, J.A. 2013. Acoustic identification of four species of bats (Order Chiroptera) in central Chile. *Bioacoustics* **22**: 165–172.

125. Russo, D. & Jones, G. 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *J. Zool.* **258**: 91–103.

126. Rydell, J., Arita, H.T., Santos, M. & Granados, J. 2002. Acoustic identification of insectivorous bats (order Chiroptera) of Yucatan, Mexico. *J. Zool.* **257**: 27–36.

127. Salsamendi, E., Aihartza, J., Goiti, U., Almenar, D. & Garin, I. 2006. Echolocation calls and morphology in the Mehelyis (Rhinolophus mehelyi) and mediterranean (R. euryale) horseshoe bats: implications for resource partitioning. *Hystrix-the Ital. J. Mammal.* **16**.

128. Schaub, A. & Schnitzler, H.-U. 2007. Flight and echolocation behaviour of three vespertilionid bat species while commuting on flyways. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **193**: 1185–1194.

129. Schmieder, D.A., Kingston, T., Hashim, R. & Siemers, B.M. 2010. Breaking the trade-off: rainforest bats maximize bandwidth and repetition rate of echolocation calls as they approach prey. *Biol. Lett.* **6**: 604–609.

130. Schnitzler, H.U., Kalko, E.K. V, Kaipf, I. & Grinnell, A.D. 1994. Fishing and echolocation behavior of the greater bulldog bat, Noctilio leporinus, in the field. *Behav. Ecol. Sociobiol.* **35**: 327–345.

131. Schoeman, C. & Jacobs, D. 2003. Support for the allotonic frequency hypothesis in an insectivorous bat community. *Oecologia* **134**: 154–162.

132. Schoeman, M.C. & Jacobs, D.S. 2008. The Relative Influence of Competition and Prey Defenses on the Phenotypic Structure of Insectivorous Bat Ensembles in Southern Africa. *PLoS One* **3**: e3715.

133. Sedlock, J.L. & Weyandt, S.E. 2009. Genetic divergence between morphologically and acoustically cryptic bats: novel niche partitioning or recent contact? *J. Zool.* **279**: 388–395.

134. Siemers, B., Kalko, E. & Schnitzler, H.-U. 2001. Echolocation behavior and signal plasticity in the Neotropical bat Myotis nigricans (Schinz, 1821) (Vespertilionidae): a convergent case with European species of Pipistrellus? *Behav. Ecol. Sociobiol.* **50**: 317–328.

135. Simmons, J.A. & O'Farrell, M.J. 1977. Echolocation by the long-eared bat, Plecotus phyllotis. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **122**: 201–214.

136. Smotherman, M. & Guillen-Servent, A. 2008. Doppler-shift compensation behavior by Wagner's mustached bat, Pteronotus personatus. *J. Acoust. Soc. Am.* **123**: 4331–4339.

137. Soisook, P., Bumrungsri, S., Satasook, C., Thong, V.D., Bu, S.S.H., Harrison, D.L., *et al.* 2008. A taxonomic review of Rhinolophus stheno and R. malayanus (Chiroptera: Rhinolophidae) from continental Southeast Asia: an evaluation of echolocation call frequency in discriminating between cryptic species. *Acta Chiropterologica* **10**: 221–242.

138. Soisook, P., Niyomwan, P., Srikrachang, M., Srithongchuay, T. & Bates, P.J.J. 2010. Discovery of Rhinolophus beddomei (Chiroptera: Rhinolophidae) from Thailand with a Brief Comparison to Other Related Taxa. *Trop. Nat. Hist.* **10**.

139. Sripathi, K., Raghuram, H. & Nathan, P.T. 2006. Echolocation sounds of the painted bat Kerivoula picta (Vespertilionidae). *Curr. Sci.* **91**: 1145.

140. Struebig, M.J., Rossiter, S.J., Bates, P.J.J., Kingston, T., Lin Oo, S.S., Nwe, A.A., *et al.* 2005. Results of a recent bat survey in Upper Myanmar including new records from the Kachin forests. *Acta Chiropterologica* **7**: 147–163.

141. Sun, K., Feng, J., Jin, L., Liu, Y. & Jiang, Y. 2008. Identification of sympatric bat species by the echolocation calls. *Front. Biol. China* **3**: 227–231.

142. Surlykke, A., Jakobsen, L., Kalko, E.K. V & Page, R.A. 2013. Echolocation intensity and directionality of perching and flying fringe-lipped bats, Trachops cirrhosus (Phyllostomidae). *Front. Physiol.* **4**: PMC3695372.

143. Surlykke, A., Miller, L.A., Møhl, B., Andersen, B.B., Christensen-Dalsgaard, J. & Buhl Jørgensen, M. 1993. Echolocation in two very small bats from Thailand Craseonycteris thonglongyai and Myotis siligorensis. *Behav. Ecol. Sociobiol.* **33**: 1–12.

144. Taylor, P.J. 1999. Echolocation calls of twenty southern African bat species. *South African J. Zool.* **34**: 114–124.

145. Teixeira, S. & Jesus, J. 2009. Echolocation Calls of Bats from Madeira Island: Acoustic Characterization and Implications for Surveys. *Acta Chiropterologica* **11**: 183–190.

146. Thabah, A., Li, G., Wang, Y., Liang, B., Hu, K., Zhang, S., *et al.* 2007. Diet, Echolocation Calls, and Phylogenetic Affinities of the Great Evening Bat (Ia io; Vespertilionidae): Another Carnivorous Bat. *J. Mammal.* **88**: 728–735.

147. Thabah, A., Rossiter, S.J., Kingston, T., Zhang, S., Parsons, S., Mya, K.M.Y.A., *et al.* 2006. Genetic divergence and echolocation call frequency in cryptic species of Hipposideros larvatus s.l. (Chiroptera: Hipposideridae) from the Indo-Malayan region. *Biol. J. Linn. Soc.* **88**: 119–130.

148. Thies, W., Kalko, E.K. V & Schnitzler, H.-U. 1998. The roles of echolocation and olfaction in two Neotropical fruit-eating bats, Carollia perspicillata and C. castanea , feeding on Piper. *Behav. Ecol. Sociobiol.* **42**: 397–409.

149. Wei, L., Han, N., Zhang, L., Helgen, K.M., Parsons, S., Zhou, S., *et al.* 2008. Wing morphology, echolocation calls, diet and emergence time of black-bearded tomb bats (Taphozous melanopogon, Emballonuridae) from southwest China. *Acta Chiropterologica* **10**: 51–59.

150. Weinbeer, M. & Kalko, E. 2007. Ecological niche and phylogeny: the highly complex echolocation behavior of the trawling long-legged bat, Macrophyllum macrophyllum. *Behav. Ecol. Sociobiol.* **61**: 1337–1348.

151. Zhang, L., Jones, G., Zhang, J., Zhu, G., Parsons, S., Rossiter, S.J., *et al.* 2009. Recent Surveys of Bats (Mammalia: Chiroptera) from China. I. Rhinolophidae and Hipposideridae. *Acta Chiropterologica* **11**: 71–88.

152. Zhang, L., Liang, B., Parsons, S., Wei, L. & Zhang, S. 2007. Morphology, echolocation and foraging behaviour in two sympatric sibling species of bat (Tylonycteris pachypus and Tylonycteris robustula) (Chiroptera: Vespertilionidae). *J. Zool.* **271**: 344–351.

153. Zhang, L., Lu, L., Zhou, S., Dai, Q., Zhao, H., Guo-hua, L., *et al.* 2002. Comparison of the Echolocation Signals in Two Species of Flat-headed Bats at Flying. *Zool. Res.* **23**: 296–300.

154. Zhang, S., Zhao, H., Feng, J., Sheng, L., Li, Z. & Wang, L. 2000. Echolocation calls of Myotis frater (Chiroptera: Vespertilionidae) during search flight. *Chinese Sci. Bull.* **45**: 1690–1692.

155. Zhang, S., Zhao, H., Feng, J., Sheng, L., Wang, H. & Wang, L. 2000. Relationship between echolocation frequency and body size in two species of hipposiderid bats. *Chinese Sci. Bull.* **45**: 1587–1590.

156. Zhu, G., Han, N., Hong, T., Tan, M., Yu, D. & Zhang, L. 2008. Echolocation Call, Roost and ND 1 Sequence Analysis of New Record of Nyctalus plancyi (Chiroptera: Vespertilionidae) on Hainan Island. *Zool. Res.* **29**: 447–451.

CAPÍTULO 3

SOUND ATTENUATION AND THE GLOBAL RICHNESS GRADIENT OF ECHOLOCATING BATS

3.1 Introduction

The geographical patterns of species richness have been extensively studied in the last decades (reviewed in Rosenzweig 1995, Willig *et al*. 2003, Field *et al*. 2009). Most studies relate the richness gradient to current or historical climatic variables (e.g. Hawkins *et al*. 2007, Davies *et al*. 2011) and/or to water and productivity (e.g. Mittelbach *et al*. 2001, Hawkins *et al*. 2003, Whittaker *et al*. 2007). Mammals show a pronounced climate-richness relationship (Buckley *et al*. 2010), primarily caused by strong tropical niche conservatism in bats (Buckley *et al*. 2010, Stevens 2011). However, some necessary predictions of this tropical niche conservatism have been put into question for some groups of New World bats (Pereira & Palmeirim 2013, Arita *et al*. 2014). Although climate and energy emerge as the correlates of species richness, several large-scale patterns are the outcome of mechanisms occurring at smaller scales (Wiens & Donoghue 2004, Tello & Stevens 2012), but processes linking these scales have proven elusive (Currie *et al*. 2004, Evans *et al*. 2005).

The abilities to fly and echolocate are assumed to be the major basis for the exceptional bat diversity (Simmons 2005, Jones & Teeling 2006). Echolocation is an active process present in all members of at least 18 of the 19 families of bats, and recent findings confirm that echolocation abilities are more widespread within this remaining family than previously thought (Gould 1988, Boonman *et al*. 2014). Navigation is the most prominent role of echolocation, probably present in all species that echolocate, and several species also use it to detect and approach food items (Griffin *et al*. 1960, Schnitzler & Kalko 2001, Korine & Kalko 2005). To form an auditory scene, bats need to dynamically integrate timing and frequency content from the target as well as several other sources of echoes in the background (Moss & Surlykke 2010, Schmieder *et al*. 2012). As a consequence, similar environments and diets might lead to similar call characteristics among the species that occupy each habitat (Schnitzler & Kalko 2001, Schnitzler *et al*. 2003, Surlykke & Kalko 2008), but in an interplay with constraints imposed by phylogenetic history (Bilski *et al*. – Chapter 1).

Most bat species produce sounds of ultrasonic frequencies (Griffin *et al*. 1960, Davies *et al*. 2013, Fenton 2013). Several studied communities are composed by bats echolocating in the range between 20 and 60 kHz, the frequency range best suited to the detection of small insects (Jones & Holderied 2007), but tropical communities also have species calling below and above those thresholds (Heller & von Helversen 1989, Fenton *et al*. 1998, Jung *et al*. 2007, 2014). Higher frequencies provide better detailing for the bat, but also lose energy more rapidly than low frequencies, which are capable of spreading for long distances (Fenton *et al*. 1998, Holderied & von Helversen 2003). Besides the spreading loss of a sound wave propagating in the open space, high frequencies are severely attenuated through atmospheric absorption (Lawrence & Simmons 1982, Kuttruff 1991, Attenborough 2007, Stilz & Schnitzler 2012). Atmospheric sound attenuation is a non-linear function of frequency, temperature and humidity (Lawrence & Simmons 1982, Attenborough 2007, Stilz & Schnitzler 2012). Its relation with sound frequency is monotonic, increasing for higher frequencies, while the relation with humidity grows until a peak, then falls back (Supplementary Figure S1). Griffin (1971) was the first to note that the range of frequencies used by insectivorous bats are the most severely attenuated in tropical conditions of temperature and humidity. He also noted that the tropics hold a suit of species that emit low frequency calls, which are much less affected by atmospheric attenuation (Griffin 1971).

As the echolocation is a self-communication mechanism, the bat needs to distinguish the echo of its own call from other sounds in the environment (Obrist 1995, Neuweiler 2003, Tressler & Smotherman 2009). Flying in close proximity with conspecifics may elicit the adoption of responses to avoid jamming, through shifts in the timing of calls (Obrist 1995), alteration of call frequency (Surlykke & Moss 2000, Ibáñez *et al*. 2004, Ratcliffe *et al*. 2004, Ulanovsky *et al*. 2004, Gillam *et al*. 2007, Bates *et al*. 2008), or both (Takahashi *et al*. 2014). Jamming avoidance has also been shown among separate species with similar calls (Necknig & Zahn 2011), and the partitioning of the sound space has been proposed as the mechanism responsible for interspecific differences in call frequency in some bat communities (Heller & von Helversen 1989, Russo *et al*. 2007, see also Kingston *et al*. 2000).

Despite being produced to acquire information, echolocation calls also convey information to eavesdroppers (Fenton 2003). It may attract conspecifics to feeding opportunities (Balcombe & Fenton 1988, Gillam 2007, Dechmann *et al*. 2009), and interspecific attraction has also been shown (Dorado-Correa *et al*. 2013). This process has commonly been viewed in a communicative context (Jones & Siemers 2010), but recent findings show that conspecifics may compete for food in an antagonistic manner, with individuals emitting calls to repel (Wright *et al*. 2014) or even disrupt the feeding approaches of its neighbors (Corcoran & Conner 2014).

Bats that use broadband calls have wider room for intra and interspecific spectral overlap, and hence are more likely to experience jamming than species that use narrowband calls (Ulanovsky *et al*. 2004). Moreover, broadband callers do not have ear cells and auditory brain centers sharply tuned to highly specialized frequencies, like those found in high duty cycle species (Vater & Kössl 2004, von Stebut & Schmidt 2004), providing them more room to vocal adaptations. However, spectral and temporal alterations of preferred echolocation characteristics disrupt the scaling of these characteristics with body size and wing beating, and possibly alter the bat's detection abilities (Speakman & Racey 1991, Fenton *et al*. 1998, Jones 1999, Holderied & von Helversen 2003, Voigt & Lewanzik 2012).

Considering that there is an optimal spectral window for food detection, and jamming avoidance responses and competition for sound space can hamper the bat's ability to find and track prey, a mechanism of acoustic niche partitioning may be responsible for the exceptional diversity of bat species crowding the tropical night skies. We here investigate the role of atmospheric sound attenuation in shaping the macroecological patterns of echolocating bat species richness. We hypothesize that attenuation provides more room to the coexistence of species that overlap in call frequencies by diminishing the interference between neighbor conspecific and heterospecific callers. First, we compare a set of models of environmental variables to determine what is the best combination of variables explaining the bat richness gradient. If atmospheric attenuation is a driver of species richness, we expect a combination of temperature and humidity to be the environmental variables that best explains the diversity of echolocating bats, and

also expect that this model does not offer a good prediction of Pteropodidae species richness. Second, we explicitly model the effect of atmospheric sound attenuation on a range of frequencies used by bats, correlating it to the species richness gradient in a non-linear fashion.

3.2 Material and Methods

We obtained geographical range maps of 1056 bat species from the IUCN global mammal assessment (IUCN 2013) to estimate the distribution of bat species richness, using a 110 x 110 km (approximately 1^{o} at the equator) equal area grid in Mollweide projection. For each grid cell, we also extracted the average annual mean temperature (Bio01), annual precipitation (Bio12), and annual mean moisture index (Bio28), from the CliMond v1.1 dataset (Kriticos *et al*. 2012), as well as the mean annual relative humidity (ARH; New *et al*. 2002), using the package `raster` 2.3-12 (Hijmans 2014) in R 3.1.2 (R Core Team 2014).

To evaluate our hypothesis, we compared 14 candidate generalized linear models fitted on the dataset excluding Pteropodidae using both Akaike Information Criterion (AIC) and spatial leave-one-out cross-validation (SLOOCV), as proposed by Le Rest *et al*. (2013, 2014). AIC and cross-validation are asymptotically convergent for independent residuals (Stone 1977), but SLOOCV ensures model selection with the best predictive ability by taking into account spatial autocorrelation in the data. Given that Buckley *et al*. (2010) showed that Chiroptera richness presents a strong relationship with mean temperature, we used it as our most basic model, through which we derived a distance buffer of 7000 km (Figure S2) for use in the SLOOCV. The other models were composed of temperature and one of the other environmental variables (Bio12, Bio28, or ARH), and the corresponding quadratic terms for one or both variables in the model (Table 1). All predictor variables were transformed into z-scores before the analyses, and all models used a negative binomial error distribution with log link function.

After selecting the best model that explains the richness gradient of echolocating bats, we refitted it using only the grid cells with no record of Pteropodidae species (183 species, Figure 1B), and used the mean squared prediction error (MSE) to compare its predictive ability in estimating the richness patterns of non-echolocating species. In addition, we evaluated the predictive ability of the model composed just by mean temperature, and the two models with log-likelihood values closest to the best one. As most Pteropodidae species occupy tropical latitudes, we repeated the process after excluding the family Phyllostomidae (173 species) – that accounts for most of the richness in the Neotropics – from the training set of echolocating bats (Figure 1).

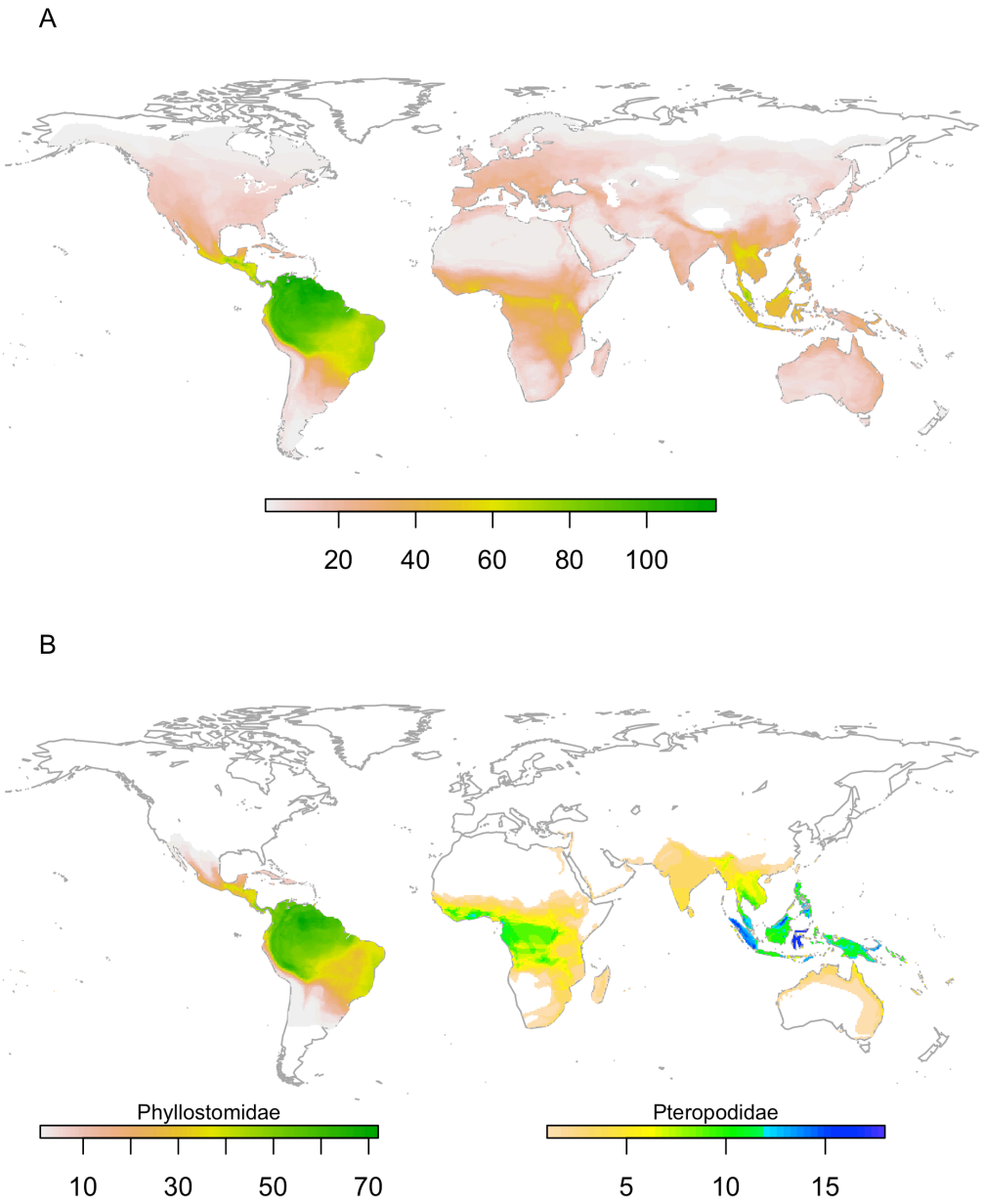


Figure 1: Species richness maps for: (A) all Chiroptera; and (B) Phyllostomidae, restricted to the New World region, and Pteropodidae, restricted to the Old World and Australasia. Note that the richness scales differ between families. The colored region in the Old World and Australasia was removed from the training set before fitting the predictive models (see text). To facilitate visualization, the maps are not projected.

To more directly investigate the relationship between sound attenuation and richness of echolocating bats, we constructed a total of 18 rasters of atmospheric sound attenuation (ASA), at a resolution of ten arcseconds, for sound frequencies between 10 and 180 kHz in 10 kHz intervals. These were constructed using the temperature and relative humidity rasters Bio01 and ARH within the formula of atmospheric sound attenuation from ISO 9613-1 (ISO 1993), assuming 1 atm pressure, and the mean values were extracted for each grid cell as above. As expected, this data show strong collinearity (Figure S3). Thus, we used variance inflation factors (VIF) to select the maximum amount of attenuation variables within the threshold VIF of 10, using the R package `usdm` 1.1-12 (Naimi 2013). This resulted in the selection of the ASA rasters of ten (ASA10), 50 (ASA50) and 180 kHz (ASA180).

These three variables were used to model echolocating bat richness within a Generalized Additive Model (GAM, Hastie & Tibshirani 1990) framework, using the R package `mgcv` 1.8-3 (Wood 2006). This method applies non-parametric smoothers to each predictor and calculates the additive component response, avoiding the necessity of assumptions about the relation between richness and ASA. However, the performance of this method can be hampered by what Wood (2006) called "concurvity", i.e. when one parameter is itself a smooth function of another parameter in the same model. Given that this was identified between the ASA values of 50 and 180 kHz, we excluded the ASA180 term from the analyses because frequencies that high are less common than those around 50 kHz (Fenton *et al.* 1998). We also built models including the moisture index Bio28 to account for other sources of sound attenuation not captured by the ASA variables. Models combining ASA10 with the other 15 ASA variables are summarized in the supplementary Table S1 and Figure S4. A negative binomial distribution was selected, with a log link function, and a gamma value of 1.4 was used to penalize model's excessive "wiggliness" (see Wood 2006). Explained deviance was used to summarize the model's ability to explain the bat richness pattern, and AIC was used to select among models using different smooth functions. The contribution of each explanatory

variable was measured through the deviance reduction associated with dropping each term from the model. After selecting the best model, we refitted it including grid cells' spatial coordinates within a bivariate spherical spline, restricted to 100 degrees of freedom, to quantify the amount of deviance left unexplained by the original model and that can be explained by the spatial dependency among grid cells. We did not include this smooth term in the first place since all other variables are spatially structured, and thus subject to significant concurvity with the purely spatial term (Hawkins & Diniz-Filho 2004).

TABLE 1: Models evaluated for explaining the richness of echolocating bats. ΔAIC was directly established from GLMs, while SLOOCV logLik was determined through spatial leave-one-out cross validation. Bold values depict the favored models pointed by each approach.

Model	**ΔAIC**	**SLOOCV logLik**
~ Bio01	7905.12	-42318.32
~ Bio01 + Bio12	3055.60	-38170.48
~ Bio01 + Bio28	2339.55	**-38125.87**
~ Bio01 + RH	3100.23	-38229.04
~ Bio01 + $Bio01^2$	7846.71	-43677.90
~ Bio01 + $Bio01^2$ + Bio12	2396.57	-39058.24
~ Bio01 + $Bio01^2$ + Bio28	1834.36	-39278.71
~ Bio01 + $Bio01^2$ + ARH	2600.56	-38886.05
~ Bio01 + $Bio01^2$ + Bio12 + $Bio12^2$	805.78	*
~ Bio01 + $Bio01^2$ + Bio28 + $Bio28^2$	**0.00**	-40580.58
~ Bio01 + $Bio01^2$ + ARH + ARH^2	2437.19	-39627.71
~ Bio01 + Bio12 + $Bio12^2$	1477.10	*
~ Bio01 + Bio28 + $Bio28^2$	444.81	-38902.45
~ Bio01 + ARH + ARH^2	2789.84	-38892.00

* Both models including the second order polynomial for Bio12 suffered from numerical instability in modeling the negative binomial dispersion parameter.

One important point must be emphasized: even though the relative humidity is commonly used in biological studies, it is not a direct measure of the quantity of water vapor in air, but a ratio of the actual moisture in relation to what could exist

without condensation in the same conditions of temperature and pressure (Anderson 1936), and does not have a direct biological impact over the organisms (Anderson 1936, Kurta 2014). The capacity of the atmosphere to hold water increases with temperature, and therefore the same relative humidity at different temperatures translate into very different atmospheric moistures. To account for this problem, we used a moisture index (Kriticos et a. 2012) that is independent of temperature (Hutchinson *et al*. 2009). For consistency with the formula of atmospheric sound attenuation (ISO 1993), we also evaluated models using a global measure of relative humidity (New *et al*. 2002), but we expect the moisture index to be a better explanatory variable in the linear models. Moreover, the moisture index accounts for condensed water in the environment, what alters the reflectance of incident sound waves by diminishing porosity (Kuttruff 1991, Attenborough 2007).

3.3 Results

Mean annual moisture index was selected through SLOOCV as the best environmental variable, in combination with temperature, to explain the richness gradient of echolocating bats. Model selection using AIC supported the model including second order polynomials for both Bio01 and Bio28 as the best one (Table 1), with all other models completely disfavored by their respective Akaike weights. On the other hand, SLOOCV supported the simpler model composed only by Bio01 and Bio28 as the best fit, and models adding the annual precipitation and ARH appeared as second and third best models, respectively. SLOOCV evaluates models by means of their predictive ability, so these were used to predict the richness patterns of Pteropodidae.

Prediction of the richness of non-echolocating bats by the selected model was worse than predictions based on two of the three other models evaluated (Table 02). Although the model composed only by mean temperature presents the lowest MSE, its better performance can be accounted for by the smaller range of predicted

values, closer to the maximum range of observed Pteropodidae richness values (Figure 02). As can be seen in the density curves, the temperature model predicted most of the richness above 20 species, a value not even encountered in any grid cell. All these models greatly overestimate the richness of non-echolocating bats, with mean values between 32 and 64 species. The same patterns hold after excluding Phyllostomidae (results not shown).

Table 2: Mean squared errors (MSE) of predictions associated with each model. Pteropodidae MSE refers to predicting this family richness based on the model adjusted to echolocating species, while Echolocating bats MSE was calculated through ten-fold cross validation.

Model	Pteropodidae MSE	Echolocating bats MSE
Bio01 + Bio28	2979.24	396.88
Bio01 + Bio12	24805.23	2292.62
Bio01 + ARH	1226.08	280.66
Bio01	842.44	525.80

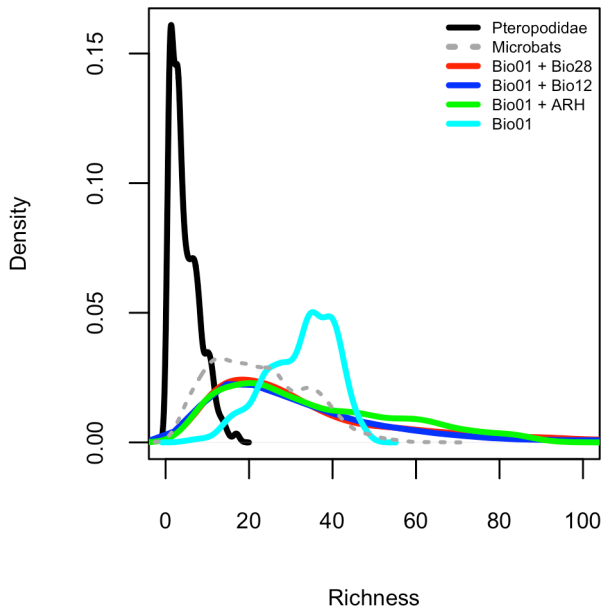


Figure 02: Density plot of the observed Pteropodidae richness gradient, and four model predictions (see text). Grey dashed line (microbats) represents the density of echolocating species in the cells with Pteropodidae species. Abscissa is truncated at 100 species, but the first two models extend beyond it.

A GAM model composed with separate smoothing parameters for each attenuation variable (ASA10, ASA50), and including Bio28, provides the best balance of explanatory power without excessive wiggliness. This model accounts for 79.2% of the deviance in the richness gradient, with a total of 58.79 estimated degrees of freedom. The shape of the response curves varied among variables (Figure 03). The model without Bio28 has a significant drop in explained deviance, accounting for 70.9% of the variance. For comparison, a GAM composed by Bio01 and ARH explains 67.6% of the deviance. ASA50 was the most important variable explaining deviance in the richness gradient, followed by Bio28 (Table 03). The model including a smooth function of spatial coordinates explains significantly more deviance in bats' richness, 96.7%. Its concurvity, however, is almost one with all other smoothing parameters. Allowing more degrees of freedom to the spatial function results in even higher explained deviances, as more localized smooth curves are created, and lead to less wiggle smooth curves to the other model terms, but with increased concurvity (Supplementary figures S5 to S8). The results shown by the other ASA variables follow the same pattern of the selected model (Table S1 and Figure S4).

Table 03: Estimated degrees of freedom, percentage explained deviance, residual deviance and drop contribution for the smooth terms included in the GAM for echolocating bat richness. The first model is the selected one that better explains the richness patters. Contribution of each term is represented by the difference in residual deviances between the favored model and the model without the respective variable. The fifth model represents the favored model plus a spatial smooth spline.

Model	**EDF**	**Explained deviance (%)**	**Residual deviance**	**Deviance difference**
ASA10 + ASA50 + Bio28	58.79	79.2	8511.5	
ASA50 + Bio28	42.75	74.7	8692.9	- 181.38
ASA10 + Bio28	48.05	65.4	9205.4	- 693.92
ASA10 + ASA50	34.71	70.9	8984.4	- 472.96
ASA10 + ASA50 +Bio28 +LatLong	138.54	96.7	7391.3	1120.2
Bio01 + ARH	33.51	67.6	9176.7	-665.22

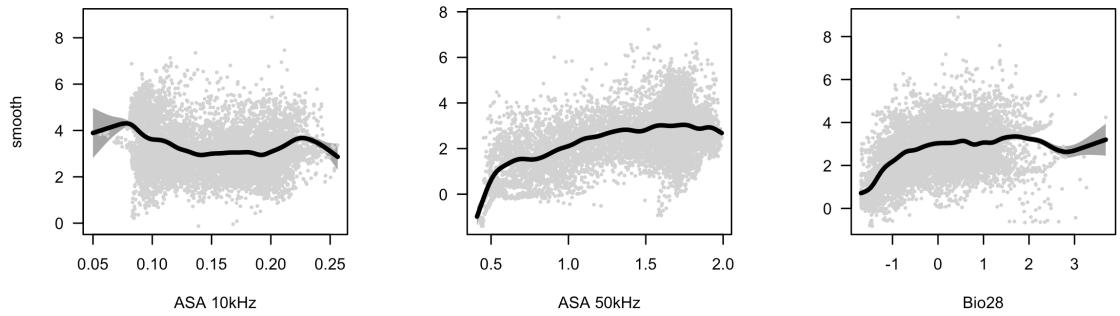


Figure 03: Response functions for the echolocating bat richness on the three environmental variables included in the GAM. The shaded areas around the smooth curves represent 95% confidence intervals, but note that it is very narrow for the major part of the curves. Points are the respective partial residuals when holding the other covariates at their median values.

3.4 Discussion

Our main goal was to evaluate the hypothesis that sound attenuation is important in determining the richness of echolocating bats, offering a mechanism through which local scale interactions mediated by the environment can integrate to structure coarse scale patterns. That prediction is supported by the finding that temperature and moisture are the best set of predictors of bat richness. If this relationship was purely mechanistic on these variables, or a matter of evolutionary processes alone (Tello & Stevens 2010, 2012), we should find this model to be a good predictor of Pteropodidae species richness. Our findings, however, point to a great overestimation of this family's richness, and the simpler model composed just by mean annual temperature as a better predictor. Models that analyze all bat species as a whole do not recognize this difference, and suggest temperature alone as the best predictor of bat richness (Buckley *et al*. 2010).

Body size may be responsible for the richness difference between Pteropodidae and other species inhabiting this region, as larger species are expected to have larger ranges (Meiri & Thomas 2007). Species richness is not correlated with body size in Chiroptera (Isaac *et al*. 2005), and whether or not Pteropodidae are significantly larger than other bats, based on its phylogenetic relationship with other groups, still waits investigation (but see Hutcheon & Garland 2004). Nevertheless, we did not find a significant difference between ranges of Pteropodidae and species of other families ($F = 62.63$, $p = 0.53$; see Supplementary material and methods), nor a relationship between body size and range area within Pteropodidae ($F_{1,154} = 0.35$, $p = 0.56$, Figure S9). At least in New World bats, there is no sign of an clade age-area relationship (Weber *et al*. 2014) nor phylogenetic signal determining range areas (Villalobos *et al*. 2013), and thus other mechanisms such as geographical constraints (Jetz & Rahbek 2002) or biotic interactions (Wisz *et al*. 2013) must be responsible for delimiting species ranges.

Although atmospheric sound attenuation is expressed by a non-linear function of temperature and relative humidity, we found the moisture index to be a better explanatory variable for the richness gradient in the linear models. Contrary to relative humidity, this variable is independent from temperature, and accounts not only for air humidity, but also for general humidity condensed in soil and vegetation (Hutchinson *et al*. 2009). That can contribute to attenuation of echolocation pulses reaching these surfaces (Yang *et al*. 2013), and alter the capabilities of bats in discerning prey close to the background (Schmieder *et al*. 2012). In the evaluated generalized additive models, the moisture index explains a significant proportion of the deviance, depicting a general trend of higher richness with increasing moisture.

Explicitly modeling sound attenuation reveals a slightly complex relationship between low frequency attenuation, namely at 10 kHz, and richness. The GAM smooth curve shows that higher species richness is encountered at both lower and higher attenuation coefficients at this frequency. We note, however, that experimental evidence must be gathered to determine if the absolute values of attenuation at this frequency have biological relevance. Attenuation at 50 kHz, on

the other hand, favors our hypothesis that higher richness is coupled with higher atmospheric sound attenuation. The variation in attenuation at this frequency is proportional to that at 10 kHz, but the biological impact is probably much higher. Disregarding other sources of sound attenuation, a bat calling at 120 dB and 50 kHz, and with a hearing threshold of 20 dB (Surlykke & Kalko 2008), spread its call for 100 m at the lower end of the attenuation gradient, but only 25 m at the more attenuating environments. This smaller range affects not just the emitter of the call, but also allows smaller inter-individual spacing. Moreover, the frequency of 50 kHz was analyzed because it represents the phylogenetic mean value for bats (Bilski *et al*. – Chapter 2), and is in the frequency window best suited for insect detection (Fenton *et al*. 1998), but several species are known to emit frequencies much higher (e.g. Holderied & von Helversen 2003, Schmieder *et al*. 2012), and thus are subject to much higher ASA.

Vegetation is also known to contribute to sound attenuation at high frequencies, both through sound wave absorption and scattering (Bullen & Fricke 1982, Yang *et al*. 2013). Adding NDVI (extracted from FAO 2008) to the selected GAM, however, adds just a minor contribution to the explained deviance, increasing it from 79.2% to 79.9% (not shown). Also, there is a high concurvity between Bio28 and NDVI, but exchanging Bio28 for NDVI diminishes by 1% the explained deviance. Vegetation probably exerts an attenuation effect more complex than what can be captured by NDVI alone, but modeling forest sound attenuation is not trivial (Fricke 1984), even more at the macroecological scale.

Bats are known to adjust echolocation time-frequency structure (Guillén *et al*. 2000, Murray *et al*. 2001, Fenton *et al*. 2011) and call intensity (Surlykke & Kalko 2008, Brinklov *et al*. 2010) to effectively probe the environment. Despite that, interspecific variation in the frequency-time domain appears to be more constrained by phylogenetic history than spatial effects (Bilski *et al*. - Chapter 1), so that closely related species have more similar echolocation call structures. In this scenario, environments with pronounced ASA provide more room to the maintenance of closely related species with minor differences in call structure, given that competition for the sound space is reduced.

Herein we provide an ecological hypothesis that can mechanistically link a process of local scale niche partitioning to the coarse scale macroecological association between species richness and environmental variables. At the large scale, attenuation can act as a condition (sensu Soberón 2007) for the species persistence in suitable areas, while at the community scale it shall act through alleviating the competition for the acoustic niche and allowing the coexistence of bat species in similar functional guilds. The macroecological pattern described in this matter must be put to test at community scale studies that thoroughly characterize the echolocation calls of all component species, as well as their activity patterns, to confirm if greater sound attenuation allows the coexistence of species with similar call frequencies.

3.5 References

Anderson, D.B. 1936. Relative humidity or vapor pressure deficit. *Ecology* **17**: 277–282.

Arita, H.T., Vargas-Barón, J. & Villalobos, F. 2014. Latitudinal gradients of genus richness and endemism and the diversification of New World bats. *Ecography.* **37**: 1024–1033.

Attenborough, K. 2007. Sound Propagation in the Atmosphere. In: *Springer Handbook of Acoustics SE - 4* (T. D. Rossing, ed), pp. 113–147.

Balcombe, J.P. & Fenton, M.B. 1988. Eavesdropping by bats: the influence of echolocation call design and foraging strategy. *Ethology* **79**: 158–166.

Bates, M.E., Stamper, S.A. & Simmons, J.A. 2008. Jamming avoidance response of big brown bats in target detection. *J. Exp. Biol.* **211**: 106–113.

Boonman, A., Bumrungsri, S. & Yovel, Y. 2014. Nonecholocating Fruit Bats Produce Biosonar Clicks with Their Wings. *Curr. Biol.* **24**: 2962–2967.

Brinkløv, S., Kalko, E. & Surlykke, A. 2010. Dynamic adjustment of biosonar intensity to habitat clutter in the bat *Macrophyllum macrophyllum* (Phyllostomidae). *Behav. Ecol. Sociobiol.* **64**: 1867–1874.

Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B., Harrison, S.P., Anacker, B.L., *et al.* 2010. Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proc. R. Soc. B Biol. Sci.* **277**: 2131–2138.

Bullen, R. & Fricke, F. 1982. Sound propagation through vegetation. *J. Sound Vib.* **80**: 11–23.

Corcoran, A.J. & Conner, W.E. 2014. Bats jamming bats: Food competition through sonar interference. *Science.* **346**: 745–747.

Currie, D.J., Mittelbach, G.G., Cornell, H. V, Field, R., Guégan, J.-F., Hawkins, B.A., *et al.* 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol. Lett.* **7**: 1121–1134.

Davies, K., Maryanto, I. & Rossiter, S. 2013. Evolutionary origins of ultrasonic hearing and laryngeal echolocation in bats inferred from morphological analyses of the inner ear. *Front. Zool.* **10**: 2.

Davies, T.J., Buckley, L.B., Grenyer, R. & Gittleman, J.L. 2011. The influence of past and present climate on the biogeography of modern mammal diversity. *Philos. Trans. R. Soc. B Biol. Sci.* **366**: 2526–2535.

Dechmann, D.K.N., Heucke, S.L., Giuggioli, L., Safi, K., Voigt, C.C. & Wikelski, M. 2009. Experimental evidence for group hunting via eavesdropping in echolocating bats. *Proc. R. Soc. B Biol. Sci.* **276**: 2721–2728.

Dorado-Correa, A.M., Goerlitz, H.R. & Siemers, B.M. 2013. Interspecific acoustic recognition in two European bat communities. *Front. Physiol.* **4**.

Evans, K.L., Warren, P.H. & Gaston, K.J. 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biol. Rev.* **80**: 1–25.

FAO. 2008. Global Pattern, Trends and Confidence Levels of Annual Sum NDVI (1981-2003). Food and Agriculture Organization of United Nations, Downloaded on 13 Frebruary 2013.

Fenton, M.B. 2003. Eavesdropping on the echolocation and social calls of bats. *Mamm. Rev.* **33**: 193–204.

Fenton, M.B. 2013. Questions, ideas and tools: lessons from bat echolocation. *Anim. Behav.* **85**: 869–879.

Fenton, M.B., Portfors, C. V, Rautenbach, I.L. & Waterman, J.M. 1998. Compromises: Sound frequencies used in echolocation by aerial-feeding bats. *Can. J. Zool.* **76**: 1174–1182.

Fenton, M.B., Skowronski, M.D., McGuire, L.P. & Faure, P.A. 2011. Variation in the use of Harmonics in the Calls of Laryngeally Echolocating Bats. *Acta Chiropterologica* **13**: 169–178.

Field, R., Hawkins, B.A., Cornell, H. V, Currie, D.J., Diniz Filho, J.A.F., Guégan, J.F., *et al.* 2009. Spatial species richness gradients across scales: a meta analysis. *J. Biogeogr.* **36**: 132–147.

Fricke, F. 1984. Sound attenuation in forests. *J. Sound Vib.* **92**: 149–158.

Gillam, E.H. 2007. Eavesdropping by bats on the feeding buzzes of conspecifics. *Can. J. Zool.* **85**: 795–801.

Gillam, E.H., Ulanovsky, N. & McCracken, G.F. 2007. Rapid jamming avoidance in biosonar. *Proc. R. Soc. B Biol. Sci.* **274**: 651–660.

Gould, E. 1988. Wing-clapping sounds of *Eonycteris spelaea* (Pteropodidae) in Malaysia. *J. Mammal.* **69**: 378–379.

Griffin, D.R. 1971. The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). *Anim. Behav.* **19**: 55–61.

Griffin, D.R., Webster, F.A. & Michael, C.R. 1960. The echolocation of flying insects by bats. *Anim. Behav.* **8**: 141–154.

Guillén, A., Juste, B. & Ibáñez, C. 2000. Variation in the frequency of the echolocation calls of *Hipposideros ruber* in the Gulf of Guinea: an exploration of the adaptive meaning of the constant frequency value in rhinolophoid CF bats. *J. Evol. Biol.* **13**: 70–80.

Hastie, T.J. & Tibshirani, R.J. 1990. *Generalized additive models*. CRC Press.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. 2007. Climate, niche conservatism, and the global bird diversity gradient. *Am. Nat.* **170**: 16–27.

Hawkins, B.A. & Felizola Diniz-Filho, J.A. 2004. "Latitude" and geographic patterns in species richness. *Ecography (Cop.).* **27**: 268–272.

Hawkins, B.A., Field, R., Cornell, H. V, Currie, D.J., Guégan, J.-F., Kaufman, D.M., *et al.* 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**: 3105–3117.

Heller, K.-G. & Helversen, O. v. 1989. Resource partitioning of sonar frequency bands in rhinolophoid bats. *Oecologia* **80**: 178–186.

Hijmans, R.J. 2014. raster: Geographic data analysis and modeling. R package version 2.3-12.

Holderied, M.W. & von Helversen, O. 2003. Echolocation range and wingbeat period match in aerial-hawking bats. *Proc. R. Soc. London. Ser. B Biol. Sci.* **270**: 2293–2299.

Hutcheon, J.M. & Garland, T. 2004. Are Megabats Big? *J. Mamm. Evol.* **11**: 257–277.

Hutchinson, M.F., Xu, T., Houlder, D., Nix, H. & McMahon, J. 2009. ANUCLIM 6.0 user's guide. Australian National University, Fenner School of Environemt and Society, Canberra.

Ibáñez, C., Juste, J., López-Wilchis, R., Núñez-Garduño, A. & Gannon, W.L. 2004. Habitat variation and jamming avoidance in echolocation calls of the sac-winged bat (*Balantiopteryx plicata*). *J. Mammal.* **85**: 38–42.

Isaac, N.J.B., Jones, K.E., Gittleman, J.L. & Purvis, A. 2005. Correlates of species richness in mammals: body size, life history, and ecology. *Am. Nat.* **165**: 600–607.

ISO. 1993. Acoustics - attenuation of sound during propagation outdoors, ISO 9613. International Organization for Standardization, Geneve, Switzerland.

IUCN. 2013. The IUCN red list of threatened species. Downloaded on 15 March 2014.

Jetz, W. & Rahbek, C. 2002. Geographic range size and determinants of avian species richness. *Science.* **297**: 1548–1551.

Jones, G. 1999. Scaling of echolocation call parameters in bats. *J Exp Biol* **202**: 3359–3367.

Jones, G. & Holderied, M.W. 2007. Bat echolocation calls: adaptation and convergent evolution. *Proc. R. Soc. B Biol. Sci.* **274**: 905–912.

Jones, G. & Siemers, B. 2010. The communicative potential of bat echolocation pulses. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **197**: 447–457.

Jones, G. & Teeling, E.C. 2006. The evolution of echolocation in bats. *Trends Ecol. Evol.* **21**: 149–156.

Jung, K., Kalko, E.K. V & Von Helversen, O. 2007. Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *J. Zool.* **272**: 125–137.

Jung, K., Molinari, J. & Kalko, E.K. V. 2014. Driving Factors for the Evolution of Species-Specific Echolocation Call Design in New World Free-Tailed Bats (Molossidae). *PLoS One* **9**: e85279.

Kingston, T., Jones, G., Zubaid, A. & Kunz, T.H. 2000. Resource partitioning in rhinolophoid bats revisited. *Oecologia* **124**: 332–342.

Korine, C. & Kalko, E. 2005. Fruit detection and discrimination by small fruit-eating bats (Phyllostomidae): echolocation call design and olfaction. *Behav. Ecol. Sociobiol.* **59**: 12–23.

Kriticos, D.J., Webber, B.L., Leriche, A., Ota, N., Macadam, I., Bathols, J., *et al.* 2012. CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods Ecol. Evol.* **3**: 53–64.

Kurta, A. 2014. The misuse of relative humidity in ecological studies of hibernating bats. *Acta Chiropterologica* **16**: 249–254.

Kuttruff, H. 1991. *Ultrasonics fundamentals and applications*. Elsevier Science & Technology.

Lawrence, B.D. & Simmons, J.A. 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J. Acoust. Soc. Am.* **71**: 585–590.

Le Rest, K., Pinaud, D. & Bretagnolle, V. 2013. Accounting for spatial autocorrelation from model selection to statistical inference: Application to a national survey of a diurnal raptor. *Ecol. Inform.* **14**: 17–24.

Le Rest, K., Pinaud, D., Monestiez, P., Chadoeuf, J. & Bretagnolle, V. 2014. Spatial leave-one-out cross-validation for variable selection in the presence of spatial autocorrelation. *Glob. Ecol. Biogeogr.* **23**: 811–820.

Meiri, S. & Thomas, G.H. 2007. The geography of body size–challenges of the interspecific approach. *Glob. Ecol. Biogeogr.* **16**: 689–693.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., *et al.* 2001. What is the observed relationship between species richness and productivity? *Ecology* **82**: 2381–2396.

Moraes Weber, M., Stevens, R.D., Lorini, M.L. & Grelle, C.E. V. 2014. Have old species reached most environmentally suitable areas? A case study with South American phyllostomid bats. *Glob. Ecol. Biogeogr.* **23**: 1177–1185.

Moss, C.F. & Surlykke, A. 2010. Probing the Natural Scene by Echolocation in Bats. *Front. Behav. Neurosci.* **4**.

Murray, K.L., Britzke, E.R. & Robbins, L.W. 2001. Variation in search-phase calls of bats. *J. Mammal.* **82**: 728–737.

Naimi, B. 2013. usdm: Uncertainty analysis for species distribution models. R package version 1.1-12.

Necknig, V. & Zahn, A. n.d. Between-species jamming avoidance in Pipistrelles? *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **197**: 469–473.

Neuweiler, G. 2003. Evolutionary aspects of bat echolocation. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **189**: 245–256.

New, M., Lister, D., Hulme, M. & Makin, I. 2002. A high-resolution data set of surface climate over global land areas. *Clim. Res.* **21**: 1–25.

Obrist, M.K. 1995. Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. *Behav. Ecol. Sociobiol.* **36**: 207–219.

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Ramos Pereira, M.J. & Palmeirim, J.M. 2013. Latitudinal Diversity Gradients in New World Bats: Are They a Consequence of Niche Conservatism? *PLoS One* **8**: e69245.

Ratcliffe, J.M., Hofstede, H.M. ter, Avila-Flores, R., Fenton, M.B., McCracken, G.F., Biscardi, S., *et al.* 2004. Conspecifics influence call design in the Brazilian free-tailed bat, *Tadarida brasiliensis*. *Can. J. Zool.* **82**: 966–971.

Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge University Press.

Russo, D., Mucedda, M., Bello, M., Biscardi, S., Pidinchedda, E. & Jones, G. 2007. Divergent echolocation call frequencies in insular rhinolophids (Chiroptera): a case of character displacement? *J. Biogeogr.* **34**: 2129–2138.

Schmieder, D.A., Kingston, T., Hashim, R. & Siemers, B.M. 2012. Sensory constraints on prey detection performance in an ensemble of vespertilionid understorey rain forest bats. *Funct. Ecol.* **26**: 1043–1053.

Schnitzler, H.-U., Moss, C.F. & Denzinger, A. 2003. From spatial orientation to food acquisition in echolocating bats. *Trends Ecol. Evol.* **18**: 386–394.

Schnitzler, H.U. & Kalko, E.K. V. 2001. Echolocation by insect-eating bats. *Bioscience* **51**: 557–569.

Simmons, N.B. 2005. An Eocene Big Bang for Bats. *Science.* **307**: 527–528.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.* **10**: 1115–1123.

Speakman, J.R. & Racey, P.A. 1991. No cost of echolocation for bats in flight. *Nature* **350**: 421–423.

Stevens, R.D. 2011. Relative effects of time for speciation and tropical niche conservatism on the latitudinal diversity gradient of phyllostomid bats. *Proc. R. Soc. B Biol. Sci.* rspb20102341.

Stilz, W.-P. & Schnitzler, H.-U. 2012. Estimation of the acoustic range of bat echolocation for extended targets. *J. Acoust. Soc. Am.* **132**: 1765–1775.

Stone, M. 1977. An asymptotic equivalence of choice of model by cross-validation and Akaike's criterion. *J. R. Stat. Soc. Ser. B* **39**: 44–47.

Surlykke, A. & Kalko, E.K. V. 2008. Echolocating Bats Cry Out Loud to Detect Their Prey. *PLoS One* **3**: e2036.

Surlykke, A. & Moss, C.F. 2000. Echolocation behavior of big brown bats, *Eptesicus fuscus*, in the field and the laboratory. *J. Acoust. Soc. Am.* **108**: 2419–2429.

Takahashi, E., Hyomoto, K., Riquimaroux, H., Watanabe, Y., Ohta, T. & Hiryu, S. 2014. Adaptive changes in echolocation sounds by *Pipistrellus abramus* in response to artificial jamming sounds. *J. Exp. Biol.* **217**: 2885–2891.

Tello, J.S. & Stevens, R.D. 2012. Can stochastic geographical evolution re-create macroecological richness–environment correlations? *Glob. Ecol. Biogeogr.* **21**: 212–223.

Tello, J.S. & Stevens, R.D. 2010. Multiple environmental determinants of regional species richness and effects of geographic range size. *Ecography.* **33**: 796–808.

Tressler, J. & Smotherman, M. 2009. Context-dependent effects of noise on echolocation pulse characteristics in free-tailed bats. *J. Comp. Physiol. A* **195**: 923–934.

Ulanovsky, N., Fenton, M.B., Tsoar, A. & Korine, C. 2004. Dynamics of jamming avoidance in echolocating bats. *Proc. R. Soc. London. Ser. B Biol. Sci.* **271**: 1467–1475.

Vater, M. & Kössl, M. 2004. The ears f whales and bats. In: *Echolocation in bats and dolphins* (J. A. Thomas, C. F. Moss, & M. Vater, eds), pp. 89–99.

Villalobos, F., Rangel, T.F. & Diniz-Filho, J.A.F. 2013. Phylogenetic fields of species: cross-species patterns of phylogenetic structure and geographical coexistence. *Proc. R. Soc. B Biol. Sci.* **280**. DOI: 10.1098/rspb.2012.2570

Voigt, C. & Lewanzik, D. 2012. “No cost of echolocation for flying bats” revisited. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **182**: 831–840.

Von Stebut, B. & Schmidt, S. 2004. Frequency processing at search call frequencies in *Eptesicus fuscus*: adaptations for long-distance target classification? In: *Echolocation in bats and dolphins* (J. A. Thomas, C. F. Moss, & M. Vater, eds), pp. 262–265.

Whittaker, R.J., Nogués-Bravo, D. & Araújo, M.B. 2007. Geographical gradients of species richness: a test of the water-energy conjecture of Hawkins *et al*.(2003) using European data for five taxa. *Glob. Ecol. Biogeogr.* **16**: 76–89.

Wiens, J.J. & Donoghue, M.J. 2004. Historical biogeography, ecology and species richness. *Trends Ecol. Evol.* **19**: 639–644.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* **34**: 273–309.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., *et al.* 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biol. Rev.* **88**: 15–30.

Wood, S. 2006. *Generalized additive models: an introduction with R*. CRC press.

Wright, G.S., Chiu, C., Xian, W., Wilkinson, G.S. & Moss, C.F. 2014. Social Calls Predict Foraging Success in Big Brown Bats. *Curr. Biol.* **24**: 885–889.

Yang, H.-S., Kang, J. & Cheal, C. 2013. Random-incidence absorption and scattering coefficients of vegetation. *Acta Acust. united with Acust.* **99**: 379–388.

3.6 Supplementary material

Figure S1: Atmospheric sound attenuation in relation to relative humidity, in air temperatures of 0°C, 5°C, 10°C, 15°C, 20°C, 25°C, 30°C and 35°C at sea level. From bottom to top, each curve represents a sound frequency between 10 and 180 kHz, in 10 kHz intervals. Dotted lines are the selected reference frequencies of 10, 50 and 180 kHz (see main text).

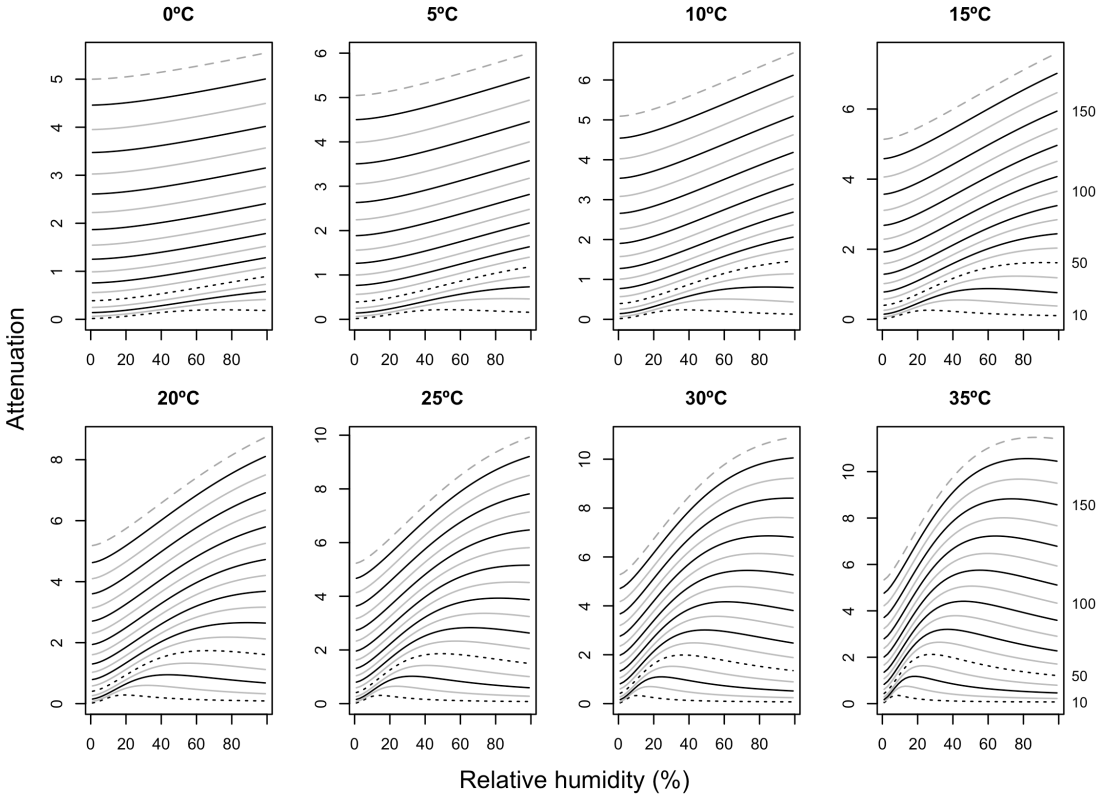


Figure S2: Semivariogram of the deviance residuals from the model between species richness and mean annual temperature.

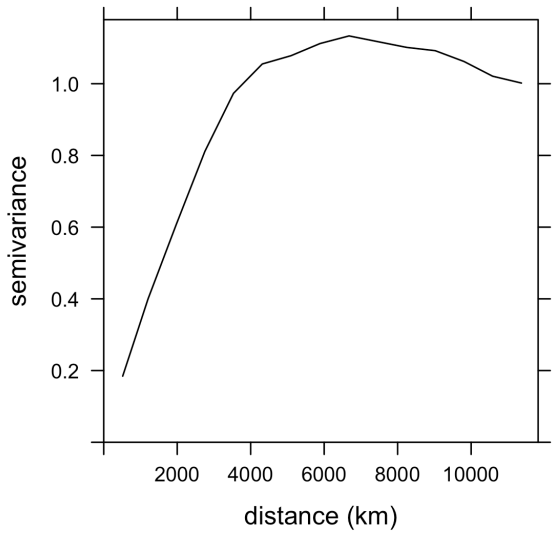


Figure S3: Correlation plot of the atmospheric sound attenuation variables.

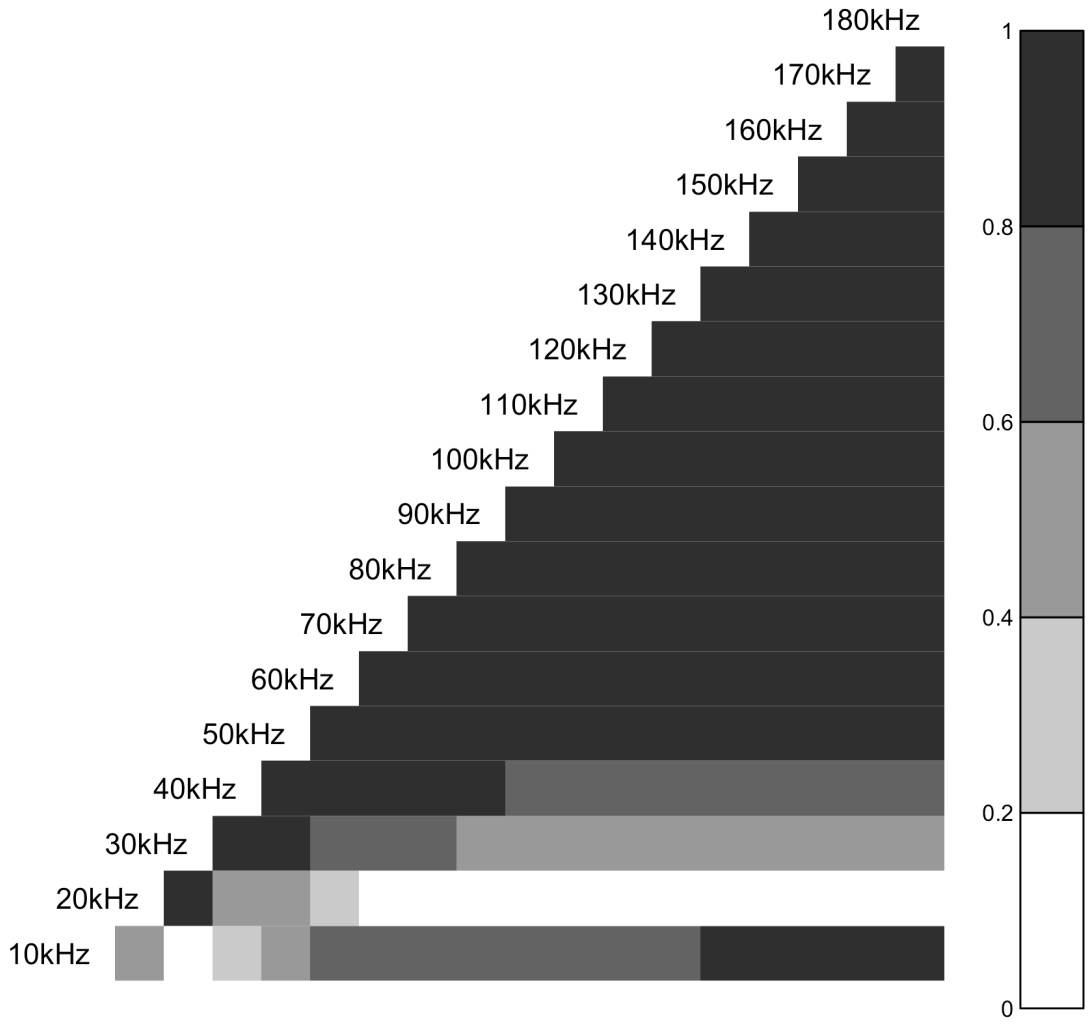


Figure S4: Response functions of the echolocating bat richness. The first and third variables, ASA10 and Bio28, are held constant among models, while the second plot depicts ASA variables between 20 and 180 kHz. The plot for ASA50 is depicted in the text.

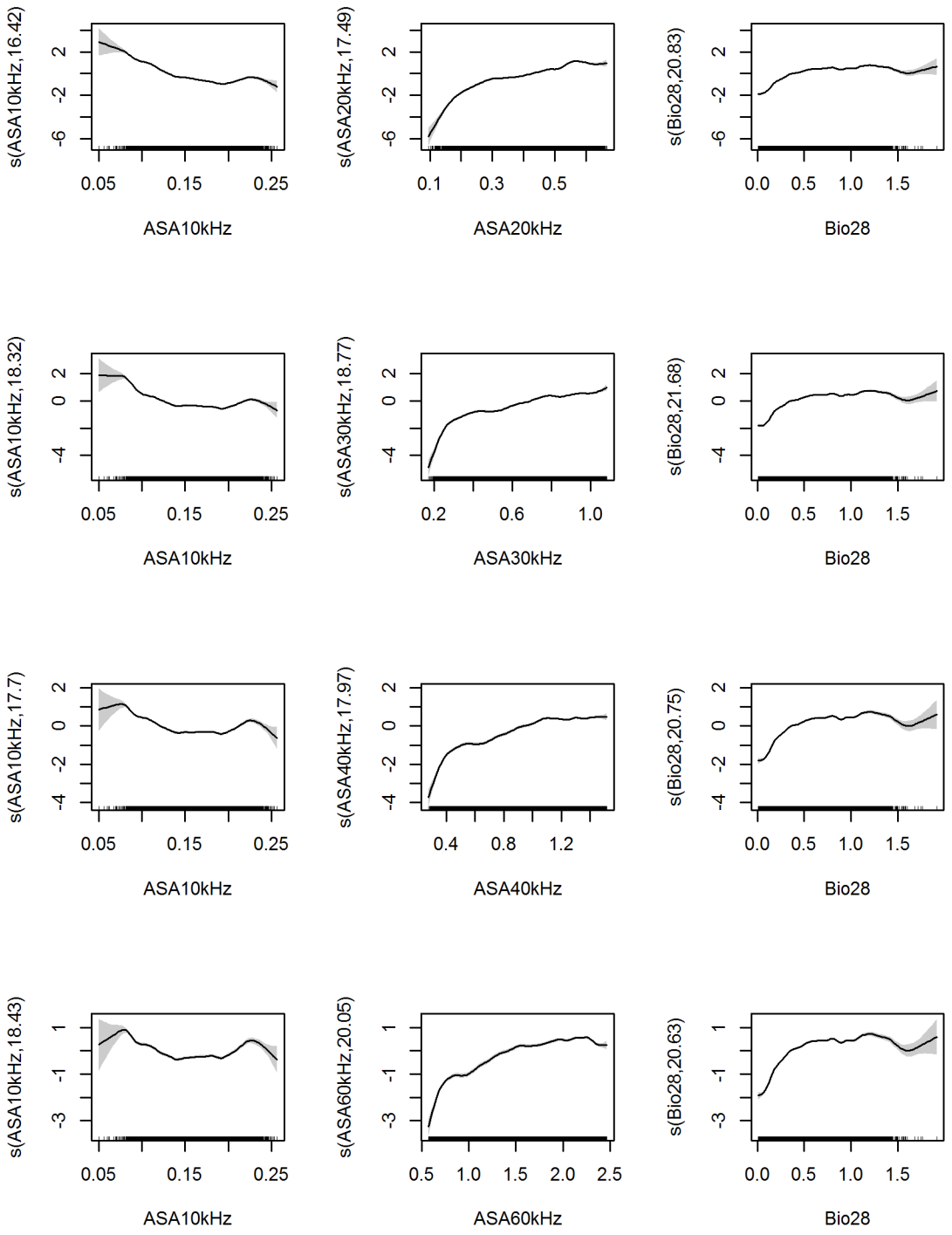


Figure S4 (continued):

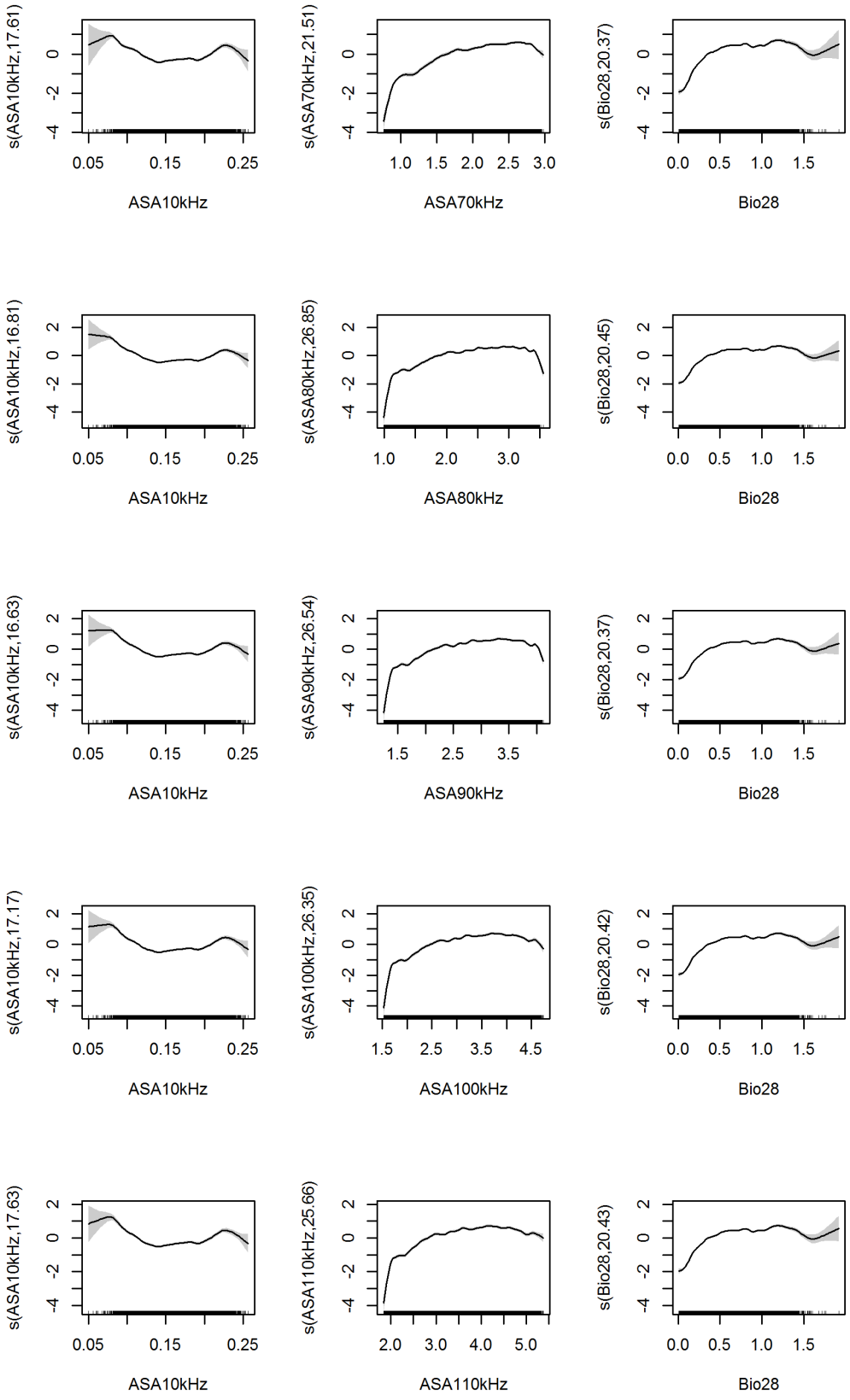


Figure S4 (continued):

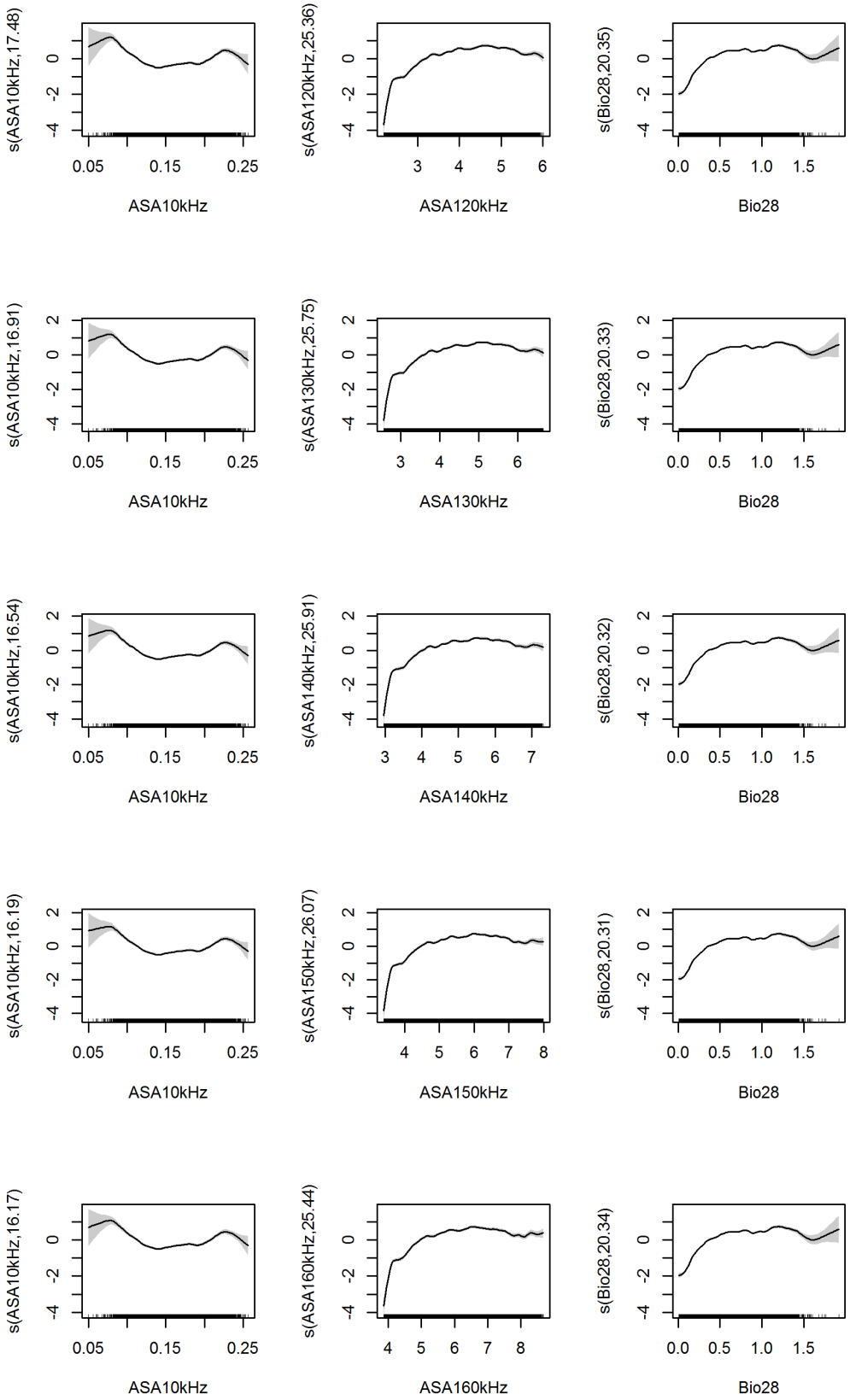


Figure S4 (continued):

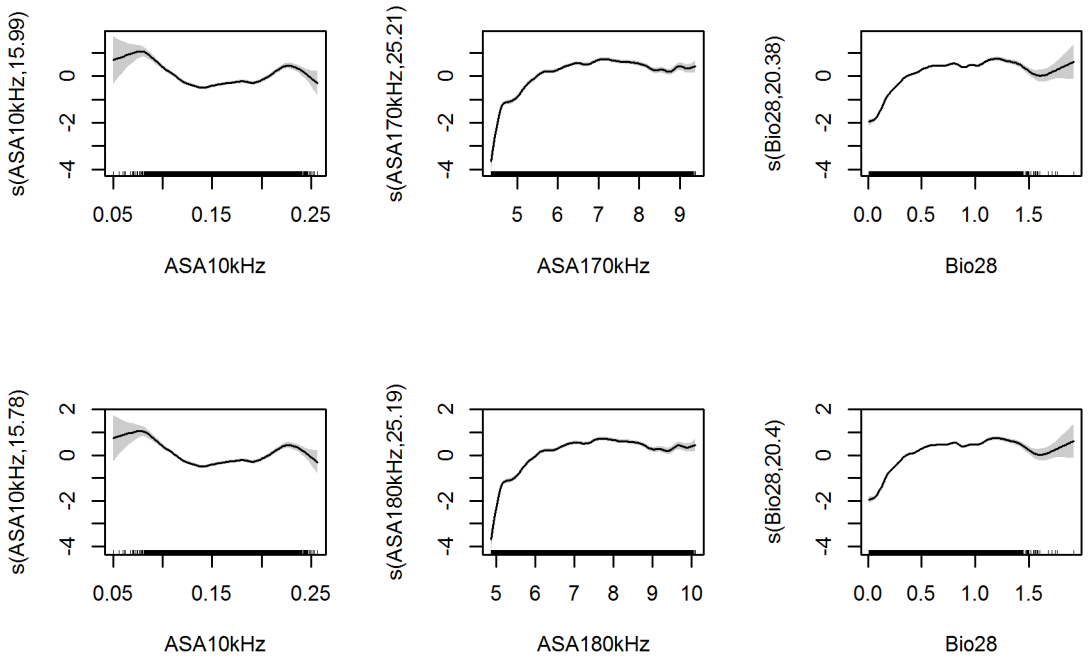


Table S1: Estimated degrees of freedom, percentage explained deviance and residual deviance for all evaluated Generalized Additive Models.

Model	EDF	Explained deviance (%)	Residual deviance
ASA 10 + ASA 20 + Bio28	78.77	55.74	8557.41
ASA 10 + ASA 30 + Bio28	78.79	59.76	8541.93
ASA 10 + ASA 40 + Bio28	78.97	57.41	8531.93
ASA 10 + ASA 50 + Bio28	79.19	58.79	8511.48
ASA 10 + ASA 60 + Bio28	79.47	60.11	8500.45
ASA 10 + ASA 70 + Bio28	79.60	60.49	8484.62
ASA 10 + ASA 80 + Bio28	79.89	65.11	8466.13
ASA 10 + ASA 90 + Bio28	79.82	64.54	8466.16
ASA 10 + ASA 100 + Bio28	79.75	64.93	8475.28
ASA 10 + ASA 110 + Bio28	79.70	64.72	8482.72
ASA 10 + ASA 120 + Bio28	79.68	64.19	8485.47
ASA 10 + ASA 130 + Bio28	79.69	63.99	8481.76
ASA 10 + ASA 140 + Bio28	79.71	63.78	8480.01
ASA 10 + ASA 150 + Bio28	79.74	63.57	8477.72
ASA 10 + ASA 160 + Bio28	79.73	62.94	8480.72
ASA 10 + ASA 170 + Bio28	79.73	62.58	8479.16
ASA 10 + ASA 180 + Bio28	79.75	62.37	8475.94

Figure S5: Response functions of the echolocating bat richness including a bivariate spatial smooth. The three upper plots represent the curves of the three investigated variables (see text). Lower plots depict four views of the spatial smooth, restricted to 100 degrees of freedom.

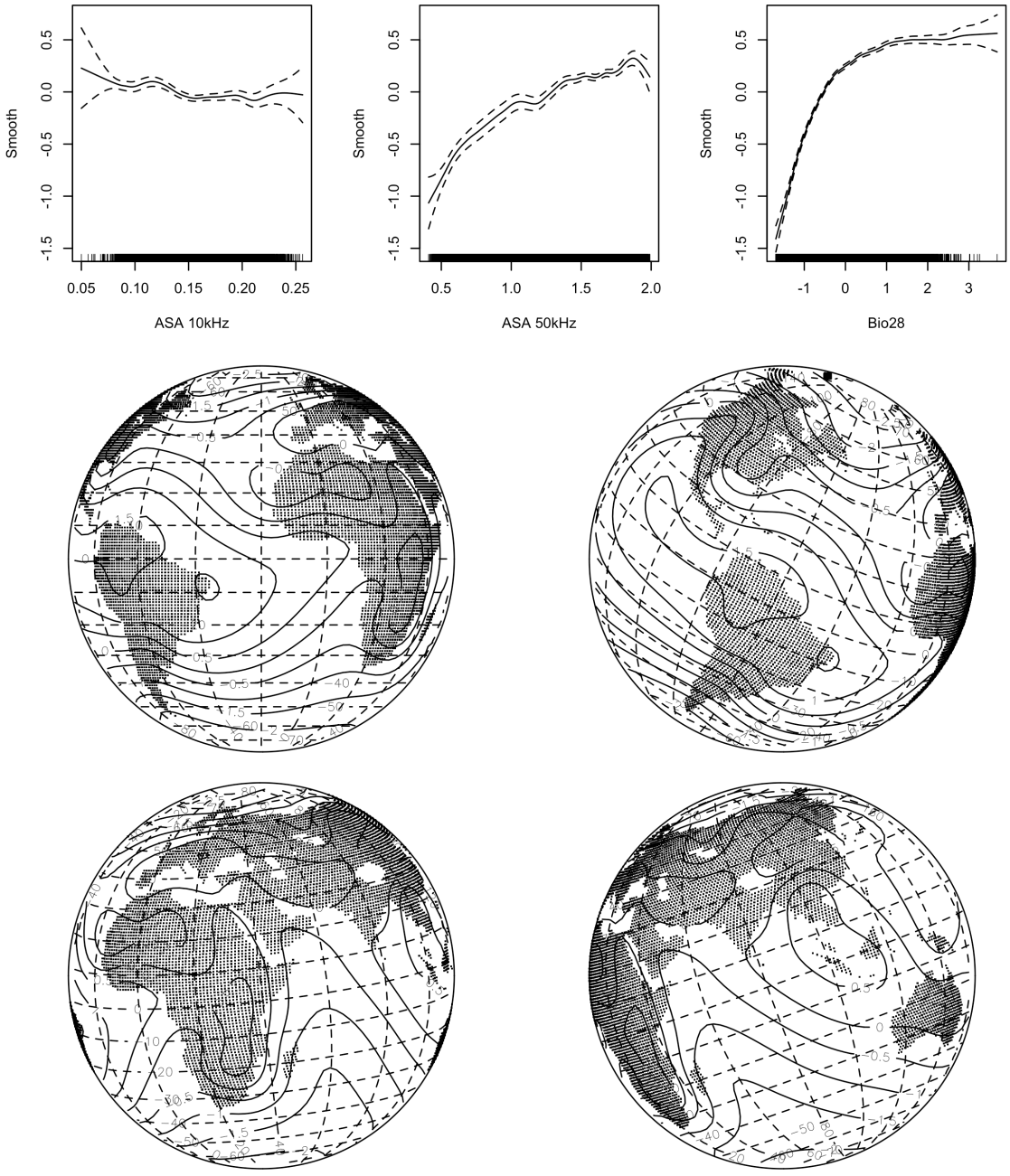


Figure S6: The same as figure S5, but allowing 200 degrees of freedom to the spatial smooth term. Note the increase in spatially restricted curves.

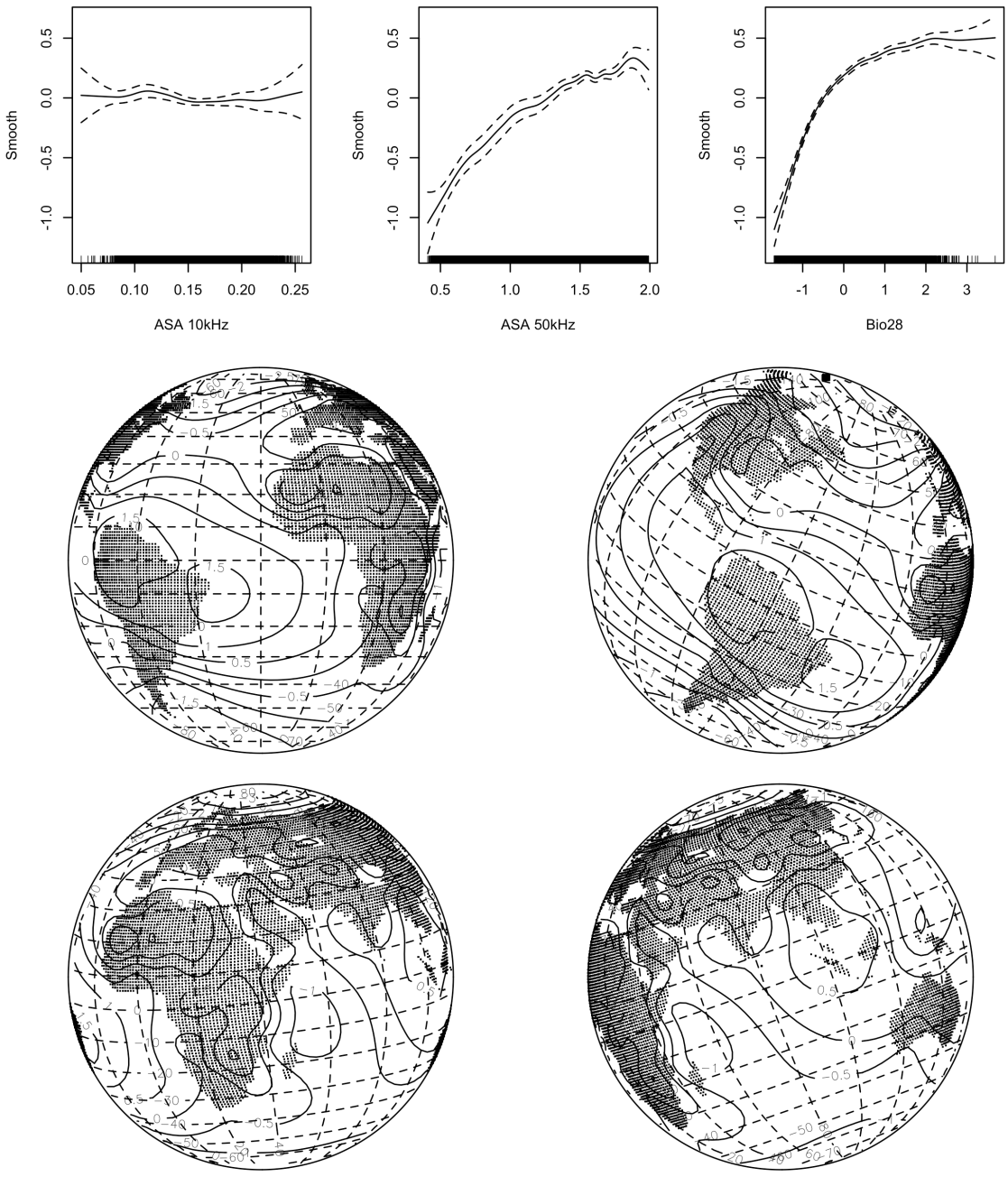


Figure S7: The same as figure S5, but allowing 300 degrees of freedom to the spatial smooth term. Note the increase in spatially restricted curves.

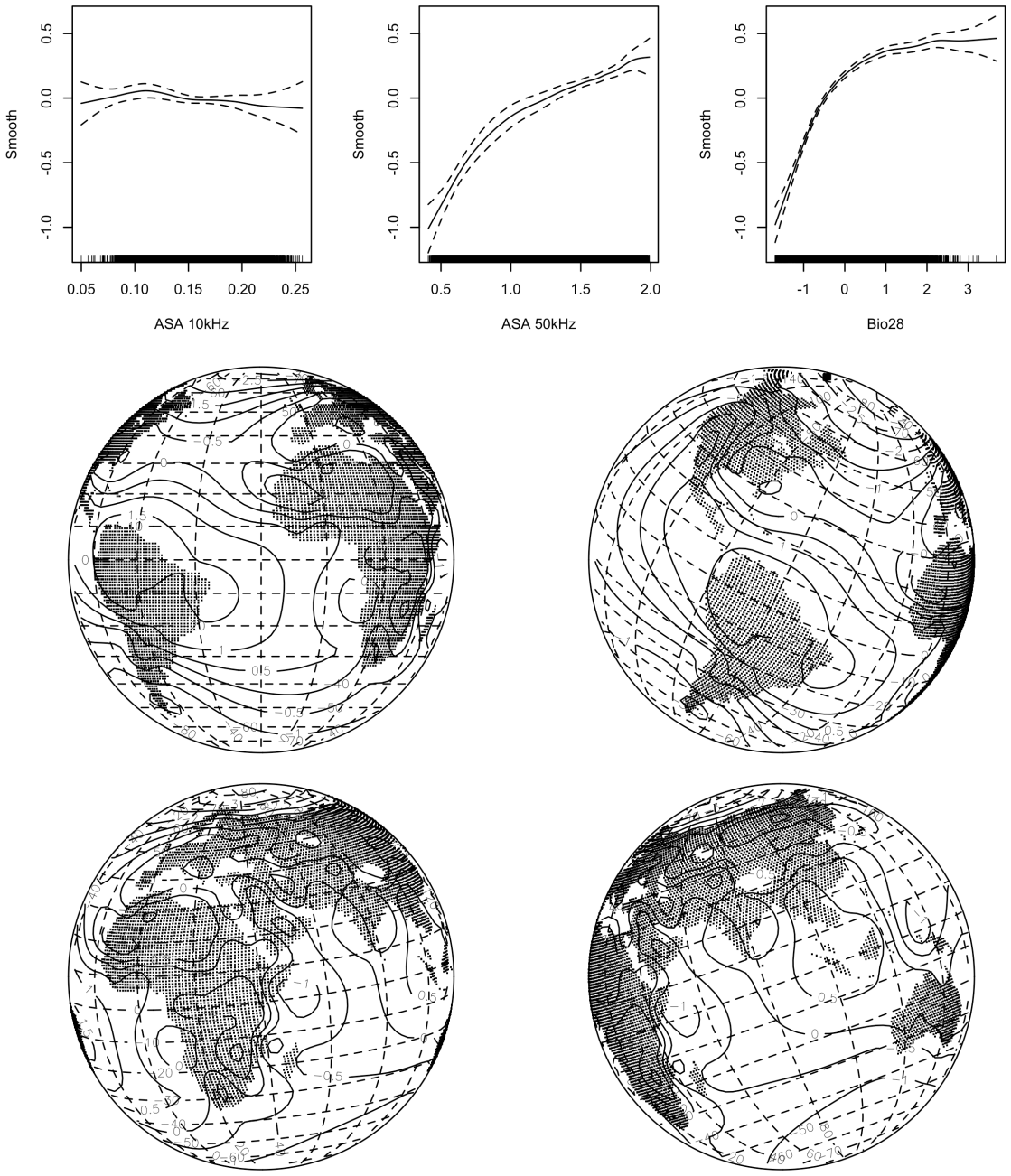
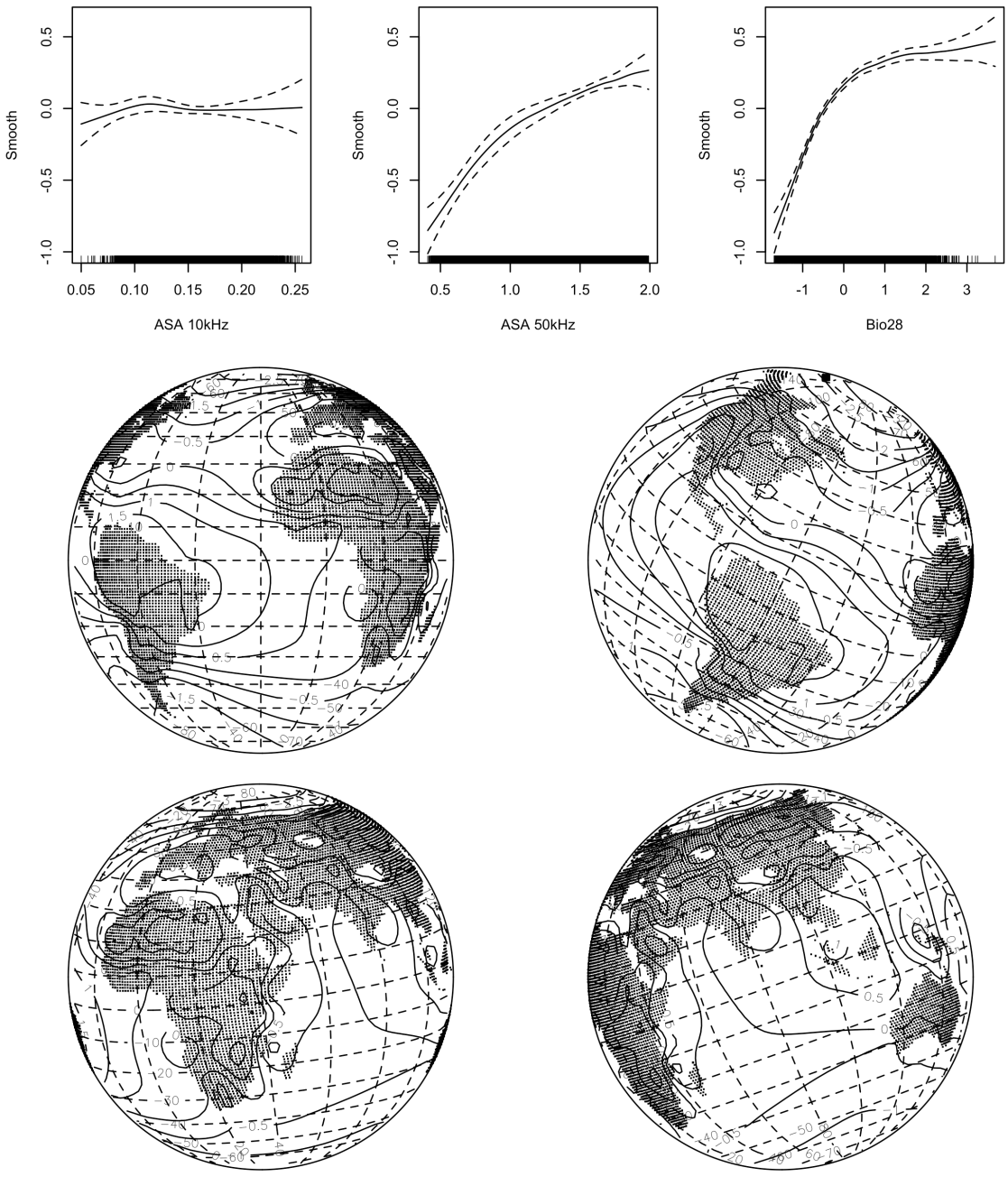


Figure S8: The same as figure S5, but allowing 400 degrees of freedom to the spatial smooth term. Note the increase in spatially restricted curves.

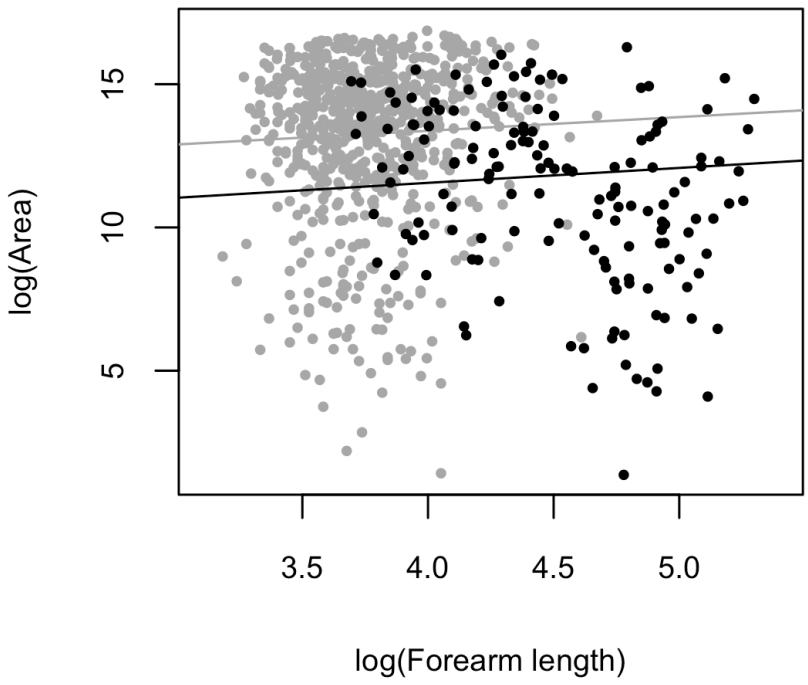


Supplementary Material and Methods

To evaluate if there is a difference between the distribution areas of Pteropodidae and echolocating species, we extracted the range areas based in the same distribution polygons (see main text), using the R package `rgeos` 0.3.8 (Bivand & Rundel 2014). To correct for the phylogenetic non-independence in the data, we used the phylogenetic tree of Fritz *et al*. (2009), and compared the mean ranges between Pteropodidae and echolocating species using the phylogenetically corrected ANOVA (Garland *et al*. 1993) function `phylANOVA` in the package `phytools` 0.4-31 (Revell 2012).

To examine the correlation between range areas and body size in the family Pteropodidae, we extracted data on the species' forearm length from the PanTHERIA database (Jones *et al*. 2009). We applied a generalized least squares regression with a phylogenetic correlation structure (`corPagel` from the package `ape` 3.1.4), to account for the phylogenetic relation among species. In all analyzes we used log transformed variables.

Figure S9: Regression of distribution range area on forearm length for 854 species. Grey dots represent 698 species of echolocating bats, while the black dots are 156 species of Pteropodidae. Regression line coefficients are: β = 0.48, t = 0.98, p = 0.32 and β = 0.52, t = 0.59, p = 0.55, respectively.



Supplementary references:

Bivand, R., & Rundel, C. 2014. rgeos: Interface to Geometry Engine - Open Source (GEOS). R package version 0.3-8. http://CRAN.R-project.org/package=rgeos

Fritz, S.A., Bininda-Emonds, O.R.P. & Purvis, A. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* **12**: 538–549.

Garland, T., Jr., A. W. Dickerman, C. M. Janis, & J. A. Jones. (1993) Phylogenetic analysis of covariance by computer simulation. *Systematic Biology*, **42**, 265-292.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., *et al.* 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**: 2648.

Paradis, E., Claude, J. & Strimmer, K. 2004. APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics* **20**: 289–290.

Revell, L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**: 217–223. Wiley Online Library.